ART. VII. EVOLUTION AND RELATIONSHIPS OF THE HETEROMYID RODENTS

WITH NEW FORMS FROM

THE TERTIARY OF WESTERN NORTH AMERICA

By Albert Elmer Wood

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INTRODUCTION

In 1931 the author discussed the phylogeny of the Heteromyidae, covering all the fossil representatives of the family then available to him. Since that time, other specimens have come to hand, some of which have already been described (Wood, 1932 and 1933). The most important portion of the new material has only now been studied, and a restudy has been made of the other members of the family. The previously known fossil forms consisted merely of jaws and teeth, or more rarely of skulls, with occasional limb bones presumably associated with them. Some of the new forms described below are of this type. Two specimens, however, are quite complete. One, from the Pliocene of Ainsworth, Nebraska, was discovered by Mr. J. H. Quinn, and kindly lent to me, for study, by the Field Museum. It consists of both rami of the lower jaw, several fragments of the skull, including the upper incisors, five cervical, five thoracic, one lumbar and six caudal vertebrae, humerus, radius, part of the ulna, the major part of the pelvis, both femora, both tibio-fibulae, astragalus, calcaneum, both naviculars, a cuneiform, and several ribs and toe bones. The other specimen, which is even more complete, was collected by the author in the summer of 1931, near the University of Nebraska Quarry at Valentine, Nebraska. With this exceptionally fine material, it is now possible for the first time to attempt a discussion of the evolution of other parts of the Heteromyidae than the cheek teeth, though only an outline can be given.

In comparing these fossil skeletons with the recent genera to which they are most nearly related, considerable use has been made of such publications as deal with their anatomy, particularly Hatt (1932) and Howell (1932). In much of the field, however, satisfactory descriptions have not been published. Hence, the anatomy of the living genera is included briefly. Furthermore, but little work has been published dealing with the detailed structure of the teeth of living heteromyids. As, in the living forms, this represents merely the end-stages of the evolutionary steps outlined by the fossils, and as the patterns are quite distinct in the various recent genera, and sometimes even in different species, the dental structure of recent genera is included in some detail. Moreover, the teeth supply the only means of comparing all the known members of the family. While an attempt has been made to arrange some of the species of the recent genera according to their phylogenetic relationships, no effort has been made to include all the living species, but merely those available in the collections of the American Museum of Natural History, and no revision of the living forms is attempted.

Very little work has been done on the anatomy and evolution of the Heteromyidae. Besides the three papers by Wood (1931, 1932 and 1933) mentioned above, the most important papers on fossil heteromyids are Cope, 1884; Dice, 1925; Gazin, 1930 and 1932; Gidley, 1922; Hall, 1930*b*; Kellogg, 1910; Matthew, 1924; and Troxell, 1923. There has been a considerable increase in the amount of available heteromyid material in the last few years. An indication of this is given by consulting Hay's Catalogs. In the first (1902) one extinct genus and one species are listed that are considered in this paper as heteromyids. In the second (1930), three genera and six species are given. In the present paper, seven genera and nineteen species are discussed. The great increase in known forms in the last few years is in large part due to more intensive collecting of small rodents.

The most important articles on recent Heteromyidae are Baird, 1857; Coues, 1877; Goldman, 1911; Grinnell, 1922; Hatt, 1932; Howell, 1932; Merriam, 1889; Osgood, 1900; and Tullberg, 1899. The papers by Hatt and Howell give the most detailed anatomical accounts. That by Coues includes the most complete summary of the classification of the family.

I am under obligations to numerous people for the assistance they have given me in the preparation of this paper. I wish to thank the Field Museum for the loan of the very interesting skeleton of *Diprionomys*. I am especially indebted to Dr. Florence Dowden Wood for many of the drawings with which this paper is illustrated. Professors W. K. Gregory and H. E. Wood have made numerous suggestions which have been incorporated in the paper, and have assisted with critical readings of the manuscript. The Department of Recent Mammals of the American Museum, and particularly Dr. R. T. Hatt, have lent me material and permitted me to study their extensive collections of recent Heteromyidae, and have also offered many helpful suggestions. The Department of Vertebrate Paleontology of the American Museum lent me the types of the fossil heteromyids in their collection, as well as undescribed material, discussed below. Mr. H. C. Raven of the Department of Comparative Anatomy has offered helpful criticisms. Mr. Harold J. Cook of Agate, Nebraska, lent me the type of *Perogna-*

thus coquorum described below. The specimens of *Mookomys formicorum* were discovered in a locality which he suggested as a possible source of heteromyids. Specimens have been lent to me by the University of California and by the California Institute of Technology. This study has been aided by grants from the Marsh Fund of the National Academy of Sciences. I wish to thank the Carnegie Museum for publishing this paper. I am indebted to the field parties of the University of Nebraska, and especially to Messrs. Johnson, McGrew and Osborne, for their extremely hospitable welcome, and for the opportunity they gave me to collect heteromyids in the vicinity of their quarry. Mr. A. D. Howard of New York University very kindly furnished me with a description of the Valentine matrix. I am grateful to Dr. G. L. Jepsen of Princeton for permission to study the specimen of *Heliscomys senex*. I wish to extend my hearty thanks to all other persons and institutions who have assisted me in any manner, and who are not specifically mentioned here.

The Heteromyidae or pocket mice are an exclusively new world, and largely western North American, family of small rodents (see maps, figs. 154-157). The living genera are *Perognathus*, the pocket mouse; *Microdipodops*, the kangaroo mouse; *Dipodomys*, the kangaroo rat; and *Liomys* and *Heteromys*, the spiny pocket mice. As can be inferred from their popular names, two of these are leaping forms, and the others scampering. In spite of the implications in their vernacular names, these animals have no affinities with the true rats and mice, perhaps being distantly related to the squirrels. Their closest living relatives are the Geomyidae, or pocket gophers, a family with a distribution very similar to that of the Heteromyidae. In body form, the pocket gophers are very different from the pocket mice, all known forms being skillful diggers, spending all, or nearly all, of their life beneath the ground. They resemble the pocket mice in many characters of soft anatomy and skeleton, the most visible being the cheek pouches, which open *outside* the mouth, known in no other groups of rodents, and from which the popular names "pocket" mice and "pocket" gophers are derived. While the burrowing activities of the pocket gophers are frequently extremely troublesome to their human rivals, the pocket mice come into very little conflict with man's interests. Their habitat is chiefly in non-arable regions; their diet principally grass-seeds. They probably are as beneficial in storing

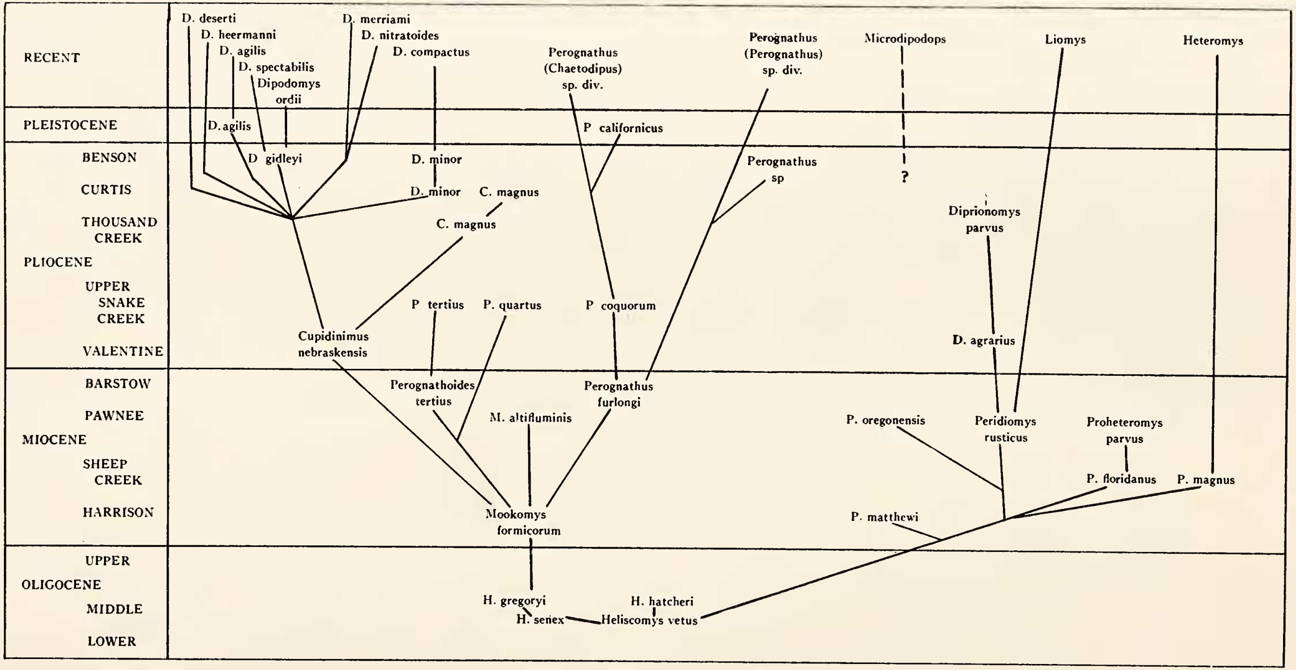


FIG. 1. Phylogenetic Chart of the Heteromyidae.

seeds where they can sprout as they are harmful in destroying those they eat.

This paper is intended as a revision of the evolution, especially the dental evolution of the Heteromyidae (see fig. 1), and includes at least a brief summary of all the known Tertiary members of the family, as well as of the recent genera. The Pleistocene forms that are known have both been referred to recent subspecies. The material is discussed in order of stratigraphic occurrence, each subfamily being considered separately.

An attempted supergeneric grouping of the forms has been made. The distinction between the Heteromyinae on the one hand, and the remaining genera on the other, is quite clear. The relations of the residual group are more difficult to determine. The foot structure of *Dipodomys* and its relatives, however, seems to be sufficiently divergent from that of the other genera to warrant retention of Coues' three subfamilies. The supergeneric groups, together with their diagnoses, are given before the discussion of the members of each subfamily. In considerable part, the superfamily and family diagnoses are modified after Coues (1875*b*, 1877).

Fig. 1a represents, in a general way, the arrangement of the more important cusps in the teeth of heteromyids. It is impossible to show all the observed cusps on a single tooth, but most of those mentioned in the text are shown on these figures, in their typical relationships. A large number of cusps are mentioned in the discussion of the ap-

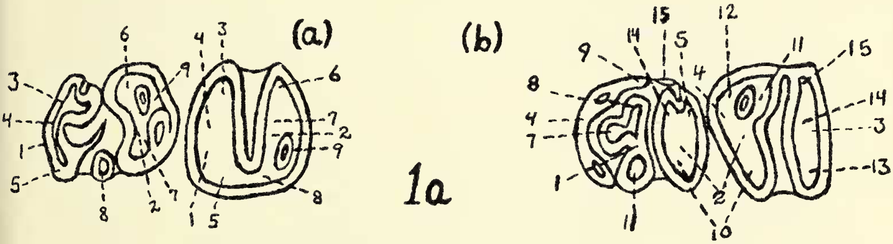


FIG. 1a. Typical heteromyid teeth showing cusp terminology adopted in this paper.
(a) LP^4—M^1. 1 = protoloph; 2 = metaloph; 3 = paracone; 4 = protocone; 5 = protostyle; 6 = metacone; 7 = hypocone; 8 = entostyle; 9 = posterior cingulum.
(b) RP_4—M_1. 1 = protolophid; 2 = metalophid; 3 = hypolophid; 4 = anterior cingulum; 5 = posterior cingulum; 7 = anteroconid; 8 = mesoconid; 9 = mesostylid; 10 = metaconid; 11 = protoconid; 12 = protostylid; 13 = entoconid; 14 = hypoconid; 15 = hypostylid.

propriate species, to which no names have been applied, as their importance is small. They can be seen on the figures of the species in question.

Order **GLIRES** Linnaeus 1758 = Rodentia Vicq d'Azyr 1792.

SUBORDER *SCIUROMORPHA* Brandt, 1855

Rodents with at least one upper and one lower premolar; masseter never passing through infraorbital opening, but extending onto zygomatic plate and the side of the rostrum; cheek teeth derivable from the *Paramys* type. New World, Eurasia and Africa. Lowest Oligocene to Recent (Probably present in Eocene).

Superfamily GEOMYOIDEA = Saccomyoidea Gill, 1872

Premolars reduced to $\frac{1}{1}$; cheek teeth primitively cuspidate and brachydont, progressively hypsodont and lophodont, first bilophate, then becoming enamel ovals, and finally reduced to enamel plates at one or both sides of the teeth; molars based on sextitubercular pattern, two of the cusps being derived from cingula; infraorbital foramen far forward on rostrum, about half way from zygoma to alveolus of incisor, not separated from masseter by large crests or ridges; mastoid greatly developed, and spread onto occipital or dorsal surfaces of the skull, or both, with corresponding reduction of the occipital; large external fur-lined cheek pouches, supplied with musculature by the platysma and other facial muscles; external form murine or some modification thereof, but not sciurine; pelage without under fur. North America and northernmost South America. Middle Oligocene to Recent.

Family GEOMYIDAE Bonaparte, 1850

Cheek teeth high crowned but rooted (Oligocene to Lower Miocene) to ever-growing; enamel progressively reduced to plates on anterior and posterior surfaces, or even to a single plate at one end of the tooth; skull massive, angular, with auditory region uninflated; interzygomatic width the greatest; palate slopes steeply downward, below level of zygoma; nasals not produced beyond incisors; zygoma strong and flaring, with stout, short malar; interorbital constriction narrower than rostrum; frontals and parietals compressed; parietals linear and far from orbits; squamosal roofing most of cerebral cavity; tympanics contracted and tubular; petrosals widely separated; occipitals broad, forming most of occiput, and not reaching top of skull; large coronoid process, erect and higher than condyle; jaw heavy;

tail shorter than body; habitus fossorial, with heavy fore limbs, small ears and eyes; pelage usually soft. North and Central America. Upper Oligocene to Recent.

Family HETEROMYIDAE

SACCOMYNA Gray, 1843 (=Heteromyidae)
DIPODOMYNA Gervais, 1853 (=Heteromyidae)
SCIUROSPALACOIDES Brandt, 1855 (=Geomyoidea—*Dipodomys*)
SACCOMYIDAE Baird, 1857 (=Geomyoidea)
HETEROMYINA Gray, 1868 (=Heteromyidae)
SACCOMYIDAE Gill, 1872 (=Heteromyidae)
HETEROMYIDAE Allen and Chapman, 1893 (=Heteromyidae)

Cheek teeth brachydont to hypsodont and even rootless; usually six cusps per molar, three on each loph; enamel rarely divided into two plates, never reduced to one; while the evolution of the teeth parallels that of the Geomyidae, at a given time the teeth of heteromyids are always more primitive; skull light, thin and papery; mastoids inflated, intermastoid diameter often being the greatest, never appreciably less than interzygomatic; interorbital space wider than rostrum; palate nearly horizontal, little if any below level of zygoma; nasals produced far beyond incisors; zygoma slender, with greatly reduced malar, almost, or quite, abutting against tympanic; frontals and parietals broad, the latter reaching, or nearly reaching, the orbits; frontal trapezoidal; parietal quadrate to pentagonal and triangular; interparietal primitively large, secondarily reduced; squamosal mostly or entirely confined to orbit; tympanic inflated or highly inflated, and vesicular; mastoids inflated and bullous, reaching top of skull, and forming part of occipital surface; occipitals contracted and limited in area on occiput, but extend onto dorsum of skull; small, sloping coronoid processes, below the level of the condyle; jaw small and weak with large, everted angle; tail as long as, or longer than, head and body; claws of manus elongate, fossorial, but fore limb slender; pelage usually coarse and frequently spinose; ears and eyes large; body form murine to ricochetal. North and Central America and northernmost South America. Middle Oligocene to Recent.

The family falls into three main groups of genera, of which one can again be subdivided. The first of the three is represented by the genus *Heliscomys*, of the Middle Oligocene, which combines certain of the characters of each of the other groups, and, in other respects, is too primitive to show the characteristics of the later subdivisions. For this reason, this genus has not been included in any of the subfamilies. Each of the other groups is characterized by certain definitive traits. Whether these groups are subfamilies or not is a matter of no great importance. They are real groups, and need to be talked about, so names of some sort are needed as handles. Coues (1875*b*) divided the family into three subfamilies, one for each of the then-known genera. These subfamilies have been ignored for the past half century, but they appear to fit the facts, as known at present, quite well.

Genus incertae sedis, perhaps ancestral to all three subfamilies, with characters common to all. Perhaps nearest to the Perognathinae.

Heliscomys Cope, 1873

Genotype: *H. vetus* Cope (1873) from the Middle Oligocene Cedar Creek Beds of northeastern Colorado.

Diagnosis: P_4 tricuspidate with a single anterior cusp, progressively developing a mesoconid; M_{1-2} quadritubercular with a broad external cingulum, progressively dividing to form two cusps, making each tooth sextitubercular; M_3 with a single stylid; P^4 with reduced paracone and weak internal cingulum; M^{1-2} of same pattern as M_{1-2}, with cingulum internal; hypocone absent in M^3, but cingulum is present; teeth bunodont and brachydont, cusps not united to form lophs; size small.

Range: Middle Oligocene of Colorado, South Dakota and Montana.

This genus is an ideal starting point for the evolution of the later Heteromyidae, with a tooth pattern which could easily give rise to that of any of the other members of the family. The ancestry of *Heliscomys* is entirely unknown, and cannot be determined until more fossils are found. There does not appear to be any described rodent, of Middle Eocene age or later, from North America, which could possibly be ancestral to *Heliscomys*, or even close to its ancestry.

At present, it seems best to leave *Heliscomys* without subfamily assignment, since most of the subfamily characters did not develop until the evolution of the teeth had proceeded further than is the case in this genus. From what is known of *Heliscomys*, it could be ancestral to any one, or more than one, of the subfamilies, and until additional material is discovered which may enable closer hook-ups with the Miocene forms, its position should remain as above, since assignment to any one of the subfamilies would tend to obscure its real relationships. It is possible that *Heliscomys* is the common ancestor of the Heteromyidae and Geomyidae, but the gap between it and the earliest geomyids is so great and the time so short as to make this virtually impossible. It is almost certain, however, that *Heliscomys*, as far as its dental development is concerned, is structurally ancestral to the geomyids.

Heliscomys vetus Cope, 1873

Fig. 7; Cope, 1884, Pl. LXV, figs. 14, 16, 16a and 17. Wood, 1931, fig. 2; Wood, 1933, fig. 7; Frechkop, 1933, fig. 7.

Holotype: A. M. N. H. No. 5461; Paratype, A. M. N. H. No. 5462, both from the Middle Oligocene Cedar Creek Beds of Colorado.

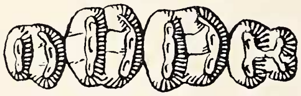
Diagnosis: P_4 tricusped; M_{1-2} with the cingulum lower than the main cusps and only incipiently subdivided into two cusps; size minute.

This species is known only from two lower jaws, from the Middle Oligocene Cedar Creek Beds of Colorado. The cingulum of the molars is definitely below the level of the other cusps, and is just beginning to be divided into two cusps (fig. 7). The other four cusps are subequal, and are all conical, with no traces of crests or ridges. The valleys between them are essentially as deep as the median valley. The premolar is triangular, with only a single anterior cusp, and no trace of a cingulum is visible. *H. vetus* is extremely minute, being one of the smallest rodents I have seen (Table II). If one follows the usually accepted belief that size must progressively increase in a given evolutionary line, the ancestral forms of this group of rodents must have been of almost microscopic size. This conception of perpetual increase is due to the fact that evolutionary studies have usually been made on large animals. As the ancestral forms of all existing mammals were small during the Cretaceous or lowest Tertiary, it follows that, in the groups that have been most thoroughly studied, there must have been a considerable increase in size. When an animal becomes of a certain magnitude, there is probably a definite selective advantage in further increase of size, up to an uncertain point, as it decreases the number of possible rivals for food as well as the number of enemies. For this reason, such forms are likely to show progressive and unbroken increase, thus illustrating "orthogenesis." To put it another way, the groups which have attracted the most attention are the ones in which the progressive increase of size was sufficiently continuous to result in animals of great size. Although the ancestral forms of a given animal will be likely to become progressively smaller the further away from the end stage we proceed, other lines of related forms will probably not evolve at the same rate. In small animals, however, there should be much less adaptive value in size, as an in-

LEFT LOWER CHEEK TEETH

RIGHT UPPER CHEEK TEETH

2



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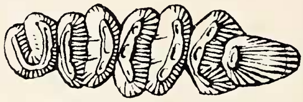

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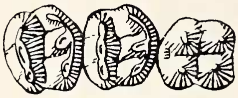

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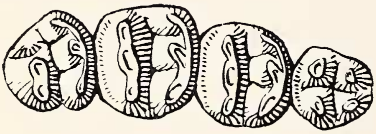

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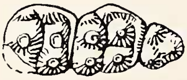


FIG. 2. *Perognathus fallax*, Amer. Mus. Nat. Hist., no. 5066, P_4—M_3 left.
FIG. 3. *P. fallax*, Amer. Mus. Nat. Hist., no. 5066, P^4—M^3 right.
FIG. 4. *Mookomys altifluminis*, Amer. Mus. Nat. Hist., no. 21360, P_4—M_2 left.
FIG. 5. *Proheteromys parvus*, Yale Mus., no. 10362, P_4—M_3 right, reversed.
FIG. 6. *Heliscomys gregoryi*, C. M. no. 10176, P^4—M^3 right.
FIG. 7. *H. vetus*, Amer. Mus. Nat. Hist., nos. 5461, 5462, P_4—M_2 left.

crease or decrease would at most merely change the group of enemies with which the animal had to deal, without altering the number to any appreciable extent.[1] A group which always remained small might show constant reversals of evolution as far as size was concerned. For this reason, it is not necessary to postulate a species of *Paramys* as small as, or smaller than, *Heliscomys*, to be its ancestor.

H. vetus is without doubt the most primitive known member of the Geomyoidea. The approximately contemporary *H. gregoryi* from Montana appears to have advanced definitely further in the elevation of the cingulum and its division into two cusps. *H. vetus* might easily be derived from a species of *Paramys* with an external cingulum in the lower teeth. Unfortunately, no such species seems to have been discovered as yet.

Heliscomys hatcheri n. sp. (Fig. 6b.)

Holotype: U. S. Nat. Mus. No. 6635, lower jaw with R M_{1-2}.

Horizon and Locality: Middle Oligocene White River Beds of Cottonwood Creek, Sioux County, Nebraska.

Diagnosis: Teeth square; external cingulum smaller and less elevated than in any other member of the family; anterior cingula small.

The specific characters listed above place this species as one of the most primitive members of the genus, and thus, of the family. The four primary cusps are subequal, and were much higher than the external cingulum. This latter was subdivided into two cusps, each more closely related to its neighbor in the main part of the tooth than to the other cingulum cusp. This suggests that the cingulum may be secondarily reduced in this species. Another possibility is that this form is closer to the stem of the geomyids than is the case with the other known members of the family, as the cingulum seems never to have attained as high a grade of perfection in the gophers as in the heteromyids. The great difference in size between this form and the earliest geomyids, as well as the close similarity of *H. hatcheri* to the other species of *Heliscomys*, in most respects, makes this last suggestion seem rather improbable.

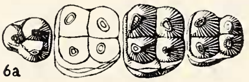
[1] Castle (1932) pointed out that among mice, large size is definitely advantageous to embryos and nursing young, in enabling them to get more than their share of food, but that the advantage was reduced or even reversed in adults.

Heliscomys senex n. sp. (Fig. 6a.)

Holotype: P. U. No. 13459, left lower jaw containing P_4 and M_{2-3}, from the Middle Oligocene Brule formation of Slim Buttes, South Dakota.

Diagnosis: Width of molars definitely greater than length; cingulum cusps lower than cusps of protomere; only one cingulum cusp on M_3; P_4 formed of three main cusps and two small antero-external ones, one of which is apparently a cingulum cusp (mesoconid) and the other a conule (metaconulid).

This species furnishes the key to the identity of the cusps of the lower premolar in the later heteromyids, and solves one of the most doubtful points of cusp homologies within the family. The three main cusps are obviously identical with those of *H. vetus*, and seem to be homologous to the protoconid, metaconid and hypoconid of the molars (fig. 6a). A posterior cingulum is present. A small cuspule is placed on the crest connecting the protoconid with the metaconid, which appears to be analogous at least with the metaconule of upper molars, and is hence referred to as the metaconulid. Anterior to this, on the buccal side of the protoconid, is a small cusp, clearly an upgrowth from a cingulum. It is reasonable to assume that one of these two cusps, growing larger, forced the protoconid toward the outside of the tooth, and formed a quadritubercular tooth like that of *Proheteromys* and *Mookomys*. The available material is insufficient to enable the question, as to which of these two cusps is homologous to the antero-external cusp of the later premolars (the mesoconid), to be settled definitely. However, among heteromyids, conules and conulids are absent except in this species alone. Styles and stylids, on the contrary, are exceptionally prevalent, most of the tooth modifications occurring in the family being connected with the origin and growth of this type of cusps. Hence, it would be more probable, *a priori*,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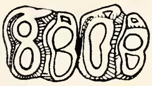

6b

Fig. 6a. *Heliscomys senex*, holotype, P. U. no. 13459, LP_4, LM_{2-3}, × 10.

Fig. 6b. *Heliscomys hatcheri*, holotype, U. S. N. M. no. 6635, RM_{1-2}, × 10.

that the stylid of P_4 of *H. senex* should give rise to the mesoconid than that the conulid should do so. Furthermore, the stylid is much more nearly in the correct position for the mesoconid. The anterior crest of the lower premolar, formed in later heteromyids by the union of the mesoconid, protoconid and later additions, may be called the protolophid (see fig. 1a).

The molars are intermediate between those of *H. vetus* and those of *H. gregoryi*, resembling the former species in the lesser height of the cingulum, and the latter in the transverse elongation of the teeth. As in *H. gregoryi*, the cingulum of the third molar supports but a single cusp, at the anterior end, the cingulum not yet having extended fully to the rear of the tooth. In M_2 of *H. senex*, as in *H. vetus*, the protostylid is much larger than the hypostylid, whereas in *H. gregoryi*, the two cingulum cusps are of about equal size. The lateral valleys of the molars are slightly less deep than are the median valleys, representing an advance over conditions in *H. vetus*. The lophization has proceeded further in M_3 than in any other tooth of *Heliscomys* that I have seen, the valley between the entoconid and hypoconid being quite shallow. Anterior cingula are present on the two molars. As the upper molars of *H. gregoryi* have an anterior cingulum, it is entirely possible that the lower molars of that species would have had a posterior one. Since there is a large entostyle in P^4 of *H. gregoryi*, it is probable that an external cingulum was present on the lower premolar, no trace of which can be seen in *H. senex*. The difference in height of the cingulum cusps, the fact that the cusps of the paramere and protomere are of equal elevation, and the presumed differences indicated above, are sufficient to demand the separation of *H. senex* from *H. gregoryi*, while the differences in the premolars and in the shape of the molars distinguish it from *H. vetus*.

Altogether, then, this species, while not solving all the problems of premolar evolution among the heteromyids, is nevertheless of considerable assistance in attaining an understanding of cusp homologies. In nearly every respect, it is intermediate between *H. vetus* and *H. gregoryi*, the only previously known members of the genus, being, if anything, slightly closer to the former. Its affinities with the Heteromyinae are definitely more remote than with the other two subfamilies (see fig. 1).

Heliscomys gregoryi Wood, 1933

Fig. 6; Wood, 1933, fig. 6; Frechkop, 1933, fig. 7.

Holotype: C.M. No. 10176 (formerly A. E. W. No. 100), from the Middle Oligocene Cook Ranch Beds of Montana.

Diagnosis: M^{1-2} sextitubercular, with cingulum cusps as large as those of the protomere, but smaller than those of paramere; P^4 Perognathine in aspect, with greatly reduced paracone; M^3 without hypocone.

This form, from the Middle Oligocene Cook Ranch Beds of Montana, is known only from one upper dentition. The cingulum cusps are lower than the paracone and metacone, though as high as the protocone and hypocone. The paracone of P^4 is greatly reduced, foreshadowing its disappearance in the Perognathinae and Dipodomyinae, at least. This species is definitely more suggestive of these two subfamilies than of the Heteromyinae, and perhaps closer to the Dipodomyinae than to the Perognathinae in the forward movement of the metacone (fig. 6), which tends to block the median valley. *H. gregoryi* is close, however, to a structural ancestor for all the later members of the family. Compared with the corresponding tooth of *Paramys*, P^4 shows rather striking differences. In the latter genus, the tooth is subtriangular, consisting of protocone, paracone and metacone, with minute conules, suggestive of the upper molars of the same form. There is a large structural gap between all of the upper teeth in the two genera, and almost as great a one in the lower molars.

Field work by H. E. Wood during the summer of 1933 definitely established the fact that the Eocene Sage Creek Formation is present in the same region as the Cook Ranch Beds, which overlie it unconformably (H. E. Wood, 1934, p. 255).

SUBFAMILY PEROGNATHINAE Coues 1875 (1875*b*)

(Name here emended; given by Coues as Perognathidinae.)

Lophs of upper premolars unite first at or near center of tooth; protoloph normally single-cusped, but sometimes secondary cusps develop; lophs of upper molars unite progressively from lingual to buccal margins; those of lower premolars unite at center of tooth, giving an X-pattern; lophs of lower molars unite primitively at buccal margin, progressively at center of tooth, forming an H-pattern; cheek teeth brachydont to hypsodont, but always rooted; pattern does not share in increase in height of crown in hypsodont forms, and hence is lost early in life; enamel always complete; $M\frac{3}{3}$ progressively reduced; upper incisor smooth or grooved; center of palate between premolars not ridged; ethmoid foramen in frontal; auditory region varies from considerably to highly inflated; bullae expand below level of grinding surface of upper cheek teeth; no median ventral foramina in caudal vertebrae; astragalus always articulates with cuboid; typically scampering, progressively saltatorial.

Genera: Mookomys, *Perognathoides*, *Perognathus* and perhaps *Microdipodops.*

Range: Lower Miocene of Nebraska, Middle Miocene of Nebraska and Montana, Upper Miocene of California, Middle Pliocene of California, Upper Pliocene of Arizona, Pleistocene of California, and Recent of British Columbia, western United States and Mexico (see chart, fig. 1, and map, fig. 155).

Mookomys Wood, 1931

Genotype: M. altifluminis Wood (1931) from the Deep River Miocene Formation of Montana.

Diagnosis: P_4 quadritubercular; M_{1-2} bilophodont and sextitubercular; cusps still very prominent on the lophs; teeth relatively low-crowned, becoming progressively higher crowned; upper incisor grooved; union of cusps of P_4 with each other of Perognathine type, but much more delayed than in *Perognathus.*

Range: Lower and Middle Miocene of Nebraska and Montana.

This genus differs from *Perognathus* chiefly in the much less lophodont character of the cheek teeth, still retaining the primitive importance of the cusps, which can be seen almost throughout life as distinct entities in the crown. This is especially well marked in the premolar. In all characters which are known, the genus could easily be ancestral to the recent *Perognathus*, as well as to other Perognathines (see fig. 1). There is no greater difficulty in deriving *Mookomys* from *Heliscomys.* The chain is strengthened by the addition of the specimens from the Harrison, discussed below, which are essentially halfway between *Heliscomys gregoryi* and *Mookomys altifluminis.* There is no trace of the H-pattern in the lower molars.

Mookomys formicorum n. sp.[1a] (Fig. 8.)

Holotype: C. M. No. 10177, RM_1; Paratypes, C. M. No. 10178, RP^4 and C. M. No. 10179, RM_2, collected by A. E. Wood from ant hills in the Lower Miocene Lower Harrison Beds, about two miles north-east of Agate, Sioux County, Nebraska, Sept. 2, 1932.

[1a] The specific name is given in compliment to the ants who originally collected the specimens.

Diagnosis: More primitive than *Mookomys altifluminis*, in its low crown and the wide separation of the individual cusps, which are sufficiently united to warrant its separation from *Heliscomys*.

The crown is beginning to be heightened, and the cusps are uniting to form lophs, thus placing the species within the limits of *Mookomys*. The cusps of the external cingulum are of the same elevation as the other four cusps (fig. 8). The two cingulum cusps are quite close together, and are separated from each other by a valley comparable in depth with those between any two cusps of the same loph. The median valley, except for the section between the protostylid and hypostylid, is much deeper than any of the lateral valleys. In these characters, this form resembles the genotype of *Mookomys*. In an unworn tooth, such as these specimens, the cusps stand out quite independently of each other, so that there is a very strong resemblance to the teeth of *H. gregoryi*. P^4 shows no trace of the paracone found in *H. gregoryi*. The tooth is symmetrical, as in *Perognathus*, but the cusps are distinct as in *M. altifluminis*. *M. formicorum* is about the same size as *M. altifluminis*, from the Deep River. One anomalous character is that the metalophid of M_1 is distinctly shorter than the hypolophid.

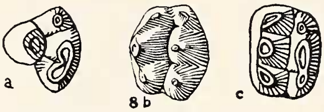


FIG. 8. *Mookomys formicorum*.
(a) C. M. no. 10178, RP^4, × 10.
(b) C. M. no. 10177, RM_1, × 10.
(c) C. M. no. 10179, RM_2, × 10.

This form seems ideally to fill the gap between *Heliscomys gregoryi* and *Mookomys altifluminis*. As far as can be told from these specimens, this species could be ancestral to both the Dipodomyinae and Perognathinae, although there is nothing to indicate definitely that such is the case. There is no very valid reason for ruling out relationship with the Heteromyinae.

Mookomys altifluminis Wood, 1931

Fig. 4; Wood, 1931, fig. 4; Wood, 1933, fig. 4.

Holotype: A. M. N. H. No. 21360, from the Deep River Miocene, seven miles south of Ft. Logan, Montana.

Diagnosis: Molars lophodont, and more high crowned, but cusps retained for a considerable time; cusps of P_4 quite distinct, the median valley being no deeper than the antero-posterior valleys.

This species is definitely Perognathine, but, at the same time, more primitive than any of the contemporary or later forms, to all of which it could have given rise, though it is probably too late actually to have done so (see phylogenetic chart, fig. 1). The cusps of P_4 show as little apparent tendency to unite into lophs as in *Heliscomys*, although the tooth has become quadritubercular as in all Perognathines (fig. 4). Most of the generic characters are equally well applicable to this species. Another specimen (A. M. N. H. No. 21409) consists of a right lower jaw with the premolar. This is much more worn than that of the holotype, and shows the typical Perognathine manner of uniting the lophs in the center of the tooth, but the cusps still remain distinct.

The skeletal material associated with the type has been restudied in connection with the two skeletons of Pliocene genera discussed below. The statement made by Wood (1931, p. 4) that the tibia and fibula were separate proves erroneous, a slight knob being distinctly visible on the shaft, marking the point at which the fibula was broken off, and to which the bones were fused. As the tooth measurements (Table II) seem to indicate an animal about the size of *Perognathus fallax fallax*, the limb bones of the two forms have been compared. The portion of the tibiofibula present in the fossil would indicate a bone of similar size and proportions to that in the recent form, but apparently slightly more progressive in the extent of fusion (see Table III). The right astragalus and the left calcaneum are present. The tibial trochlea of the astragalus is shorter than the fibular, as in other heteromyids and in *Paramys*. As in *Perognathus*, there was no naviculo-calcaneal contact, which differentiates these forms from the Dipodomyinae, in which it is characteristically present. In *Paramys*, apparently both the calcaneal-navicular and the astragalo-cuboid contacts occur, neither being greatly developed. The ectocuneiform is shaped as in *Perognathus*, though slightly larger than in *P. f. fallax*. The outline of the bone is more even than in *Paramys*. The distal half of the humerus is preserved, and is almost identical with that of *Perognathus*, except that the deltoid process extends slightly further distad in *Mookomys*, a more primitive condition, approaching what we find in *Paramys*. The olecranon is shorter in *Mookomys* than in *Perognathus*, but otherwise the part of the ulna represented seems indistinguishable in the two forms. The pes, as far as determinable, is similar to that of *Perognathus*. These comparisons indicate an animal close to *Perognathus* in most of its characters, but definitely more primitive in nearly every respect. With the exception of the percent of fusion of the tibia and fibula (which is within the range of variation of *Perognathus*), every character in which the skeleton of *Mookomys* differs from that of *Perognathus* shows an approach toward *Paramys*. In spite of this, the skeleton of *Mookomys* is a typical heteromyid one, showing fundamental differences from that of *Paramys*.

Perognathoides new genus

Genotype: Diprionomys quartus Hall, 1930b, from the Pliocene Thousand Creek Beds of Esmeralda County, Nevada.

Diagnosis: Teeth with Perognathine pattern; P^4 with two accessory cuspules in protoloph, one buccal and one lingual; teeth higher crowned than in the more primitive species of *Perognathus* or than any other Tertiary Perognathine; P$\frac{4}{4}$—M$\frac{2}{2}$ subequal; upper incisors asulcate.

The forms included in this genus are definitely related to *Perognathus*, although they are probably collaterals rather than direct ancestors, because of the more advanced hypsodonty of the cheek teeth, and the different specialization of P^4, as well as the fact that they are later than the earliest known species of *Perognathus*. The difference between grooved and smooth incisors is considered by taxonomists dealing with living rodents as being in itself a generic distinction. If this difference is caused by a single gene mutation, as seems likely from its widespread occurrence in independent lines of rodents, its evolutionary importance might be questioned. However, taken together with the pseudo-Heteromyine pattern of P^4, and the high crowns, it seems reasonable to separate this group of species. If the buccal cuspule of P^4 should be the paracone, it would suggest independent derivation from *Heliscomys*, a suggestion borne out, from the point of view of orthodox paleontology, by the asulcate incisors, which could not have evolved from the grooved ones of *Mookomys* without reversal of evolution. The presence of the accessory cusps of P^4 would rule *Perognathoides* out from possible ancestry to *Perognathus*, unless on the basis of the ingenious theory suggested by Schreuder (1933).

The exact relationships of the two species referred to this genus cannot be definitely determined without more material than is at present available. The characters listed below as specific characters for *P. tertius*, however, all seem to represent distinct advances in specialization over *P. quartus*, some paralleling *Perognathus*, and some, *Dipodomys*.

Perognathoides quartus (Hall)

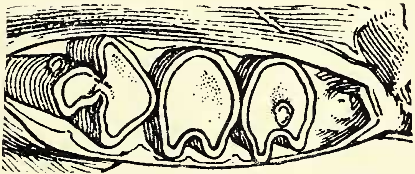
DIPRIONOMYS QUARTUS Hall 1930*b*

Figs. 9-10; Hall, 1930, figs. 5-8.

Holotype: U. Cal. Coll. Vert. Pal. No. 29639, from the Fish Lake Valley Pliocene Beds of Esmeralda County, Nevada.

Diagnosis: Size large; P^4 with protostyle and buccal style; teeth less hypsodont than in the other known species; $P\frac{4}{4}$ subequal to $M\frac{1}{1}$; little reduction of $M\frac{3}{3}$; P$_4$ becomes circular when worn; infraorbital foramen far forward.

This species is strongly suggestive of *Perognathus* in all its dental characters except those of P^4. The accessory cusps of this tooth are of doubtful significance, but are probably at least specific and very possibly generic characters. The upper incisors show no evidence of any sulci. The metaloph of P^4, both lophs of M^1, and the protolph of M^2, are all nearly of equal width (Table II). The protoloph of P^4 unites with the center of the metaloph (fig. 9), which serves to unite this genus with the Perognathinae, counterbalancing the tricuspidate



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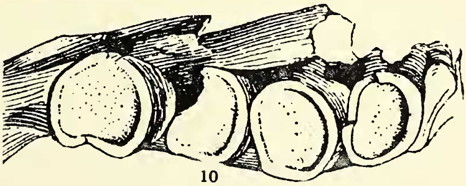

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FIG. 9. *Perognathoides quartus*, After Hall, 1930*b*, RP^4—M^2, × 10.

FIG. 10. *Perognathoides quartus*, After Hall, 1930*b*, RP$_4$—M$_3$, × 10.

character of the loph, which is a characteristic of the Heteromyinae. The lophs of the upper molars fuse progressively from the lingual to the buccal sides. The external folds of the upper cheek teeth are preserved for a considerable time. The enamel lake in RM^2 of the holotype is a minor accident, due to the union of the paracone and metacone slightly before the complete destruction of the median valley. It is probably an individual character to which no particular significance can be attached, as it is in *Perognathus*, though it may be of specific value. The presence of this lake is verbally suggestive of affinities with the Heteromyinae, but it is merely a superficial resemblance, similar to the resemblance of P^4. In the Heteromyinae, when the paracone and metacone first unite, it is at their buccal margin. In this instance, it is between their lingual tips. The two lophs are not separated in the center and approximated at either end, but rather the flanks of the paracone and metacone extend further into the median valley than do the spaces between the proto- and paracones on the one hand, and between the meta- and hypocones on the other. Furthermore, as in *Perognathus*, the lake in *Perognathoides* is an extremely evanescent character, whereas that in the Heteromyinae is of considerable duration. Moreover, as indicated above, the fundamental character of P^4 is Perognathine. This is an instance of the dangers awaiting the taxonomist who bases his classification on a single character rather than the totality of characters of the animals involved.

The lower jaw, U. Cal. Coll. Vert. Pal. No. 29631, doubtfully referred to this species by Hall (1930*b*) may well be correctly allocated, although it is so badly worn as to make any assignment uncertain (fig. 10). The relative sizes of the teeth, with P_4—M_2 subequal and M_3 only slightly smaller than the others, is certainly suggestive of *P. quartus*. The two lophs of P_4 appear to be nearly the same size. M_2 is wider than M_1, which may be due merely to the atypical development of M_1, which is extremely crowded by the adjacent teeth. The anterior portion of the masseteric crest is nearly horizontal.

The general proportions of the teeth most nearly resemble those of *Heliscomys gregoryi*. The nearly equal width of the three anterior teeth in each jaw of *P. quartus* seems quite characteristic, as does the lack of reduction of $M\frac{3}{3}$.

Perognathoides tertius (Hall)

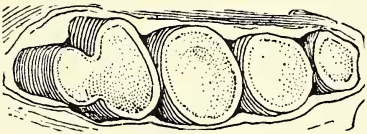
DIPRIONOMYS TERTIUS Hall 1930*b*

Figs. 11-12; Hall, 1930*b*, figs. 2-4.

Holotype: U. Cal. Coll. Vert. Pal. No. 29632, from the Fish Lake Valley Pliocene Beds of Esmeralda County, Nevada.

Diagnosis: Crowns high; M_2 equal in width to M_1; P_4 much narrower; M^3 definitely reduced; marked depression between M_3 and base of coronoid process, without a foramen; P^4 wider than M^2.

The teeth are so highly worn in the holotype of this species that nearly all characters of any diagnostic value have been destroyed. The protoloph of P^4 is definitely Perognathine, uniting with the center of the metaloph. How many cusps there were in the protoloph cannot be determined from such worn material. M^1 and the metaloph of P^4 are of about the same width. M^2 is definitely narrower and M^3 considerably so (fig. 11). P_4 is larger than in *Perognathus*, being subequal in area to either of the first two molars. The masseteric crest is similar to that of *P. quartus*. The depression between M_3 and the coronoid process helps to distinguish this species from *Perognathus* in the absence of upper incisors and unworn cheek teeth, although depressions of this sort do occur in some species of *Perognathus*. The teeth are more high crowned than in *Perognathus*. The development of the depression at the base of the coronoid process and the progressive hypsodonty are parallelisms to the similar evolution in *Dipodomys*, from which this species is separated by the distinctive character of P^4. These same characters are also resemblances to *Microdipodops*, which, however, has only a single cusp in the protoloph of P^4.



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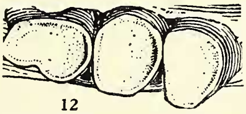

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FIG. 11. *Perognathoides tertius*, After Hall, 1930*b*, LP^4—M^3, × 10.
FIG. 12. *Perognathoides tertius*, After Hall, 1930*b*, RP_4—M_2, × 10.

Several additional specimens, from the Barstow Miocene of San Bernardino County, California, are referred to this species by Hall (1930*a*). Hall (1930*a*, fig. 4) figures two teeth (U. Cal. Coll. Vert. Pal. No. 28541) from the Barstow Beds, which appear to represent RP_4—M_1 of a Perognathine. Tentatively they may be referred to *Perognathoides tertius*, which is the only described heteromyid from this formation.

Perognathus Maximilian, 1839

Synonymy:

CRICETODIPUS Peale, 1848
ABROMYS Gray, 1868
OTOGNOSIS Coues, 1875
CHAETODIPUS Merriam, 1889

Figs. 2-3, 13-29; Baird, 1857, Pl. 51, figs. 3f and g, 4f and g; Merriam, 1889, Pl. 4, figs. 1-6; Tullberg, 1899, Pl. 27, figs. 27-30; Wood, 1931, fig. 5; Wood, 1933, figs. 2-3; Frechkop, 1933, fig. 7.

Genotype: P. fasciatus Maximilian 1839, from the Missouri River near the mouth of the Yellowstone River.

Diagnosis: Perognathine tooth pattern; sulcate upper incisor; teeth progressively high crowned but rooted; protoloph of P^4 always a single cusp uniting with the central part of the metaloph; P_4 nearly always four cusped, generally developing an X-pattern; molars generally without H-pattern; $M\frac{3}{3}$ reduced; $dP\frac{4}{4}$ relatively simple, especially dP_4; no foramina and usually no pit between M_3 and the base of the coronoid process; auditory region slightly to rather inflated; body form murine; locomotion scampering to sub-ricochetal.

Range: Miocene of Nebraska and California; Pliocene of Nebraska and Arizona; Pleistocene of California; Recent of British Columbia, western United States and Mexico (see map, fig. 155).

Some specimens of *Perognathus* approach *Dipodomys* in one respect or another, the total number of such instances being rather large. No one form combines these, however, to a sufficient extent to warrant the supposition that this genus is ancestral to the kangaroo rats. The same series of characters are likewise suggestive of relationship with *Microdipodops*, as are also some additional characters which help to distinguish *Perognathus* from *Dipodomys*, but it seems probable that the kangaroo mice have also been a distinct line for some time. All of these forms show a great deal of parallelism with each other, as will be brought out below. The exact relationships of the recent genera to each other and to the fossil genera are still difficult to determine.

Sufficient fossils are now known to enable one to picture the main outlines of the evolution of the family and to develop a fairly accurate picture of the trends in dental evolution, but many important points still remain to be elucidated.

The skull of *Perognathus* is inflated to a variable extent, the skull index[2] of some forms, as *P. apache*, approaching those of the more primitive species of *Dipodomys*, whereas in others, as *P. spinatus*, the skull is much more primitive, the mastoid being but slightly inflated, approaching *Liomys* in general proportions (see Table IV). The variations in the size of the interparietal, correlated with the variations in the mastoids, are also considerable (Table IV). The species of the subgenus *Perognathus* have compressed interparietals and inflated bullae, whereas in *Chaetodipus* they are uninflated and uncompressed. The interparietal is occasionally found paired, even in aged animals, but the frequency is much lower than in *Liomys* (see below, p. 200), having been observed but four times in about 250 skulls. There is a broad contact on the dorsum of the skull between the squamosal and the parietal. In *Dipodomys*, the squamosal is almost entirely crowded out of the dorsum of the skull by the lateral expansion of the frontal and parietal and the exceptional inflation of the mastoid. In this respect, *Perognathus* resembles *Microdipodops*, some species even showing a slight notch in the parietal into which the temporalis has carried the squamosal, though it is not as large as in the latter genus. The parietal sends a process laterad between the squamosal and the mastoid, separating them for a distance which varies in different species. In some forms, as *P. penicillatus eremicus*, it is as short as in *Dipodomys*, whereas in *P. lordi* and *P. m. merriami*, on the contrary, it is as long as in *Microdipodops*, nearly separating the squamosal from the mastoid. In *Perognathus*, the alisphenoid extends slightly higher than the glenoid, and abuts against the frontal for about a third of the intra-orbital length of the latter. In *Dipodomys*, the main body of the alisphenoid does not extend above the glenoid, although a narrow process reaches antero-dorsad to meet the

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[2] This index is a useful measure of the amount of inflation of the auditory region. The maximum width of the skull is measured, either across the zygoma or across the auditory region, whichever is the greatest. The skull length is the distance from the tip of the nasal to the projection on the midline of the most posterior part of the skull. The index is the width times 100, divided by the length.

frontal, separating the squamosal and orbitosphenoid. In *P. parvus*, there is a process from the alisphenoid reaching toward, but not meeting, a similar process of the bulla, suggestive of the situation in *Microdipodops* (see below, p. 113). There is an ethmoid foramen in the frontal, near the dorsal margin of the orbit. The anterior margin of the external auditory meatus is generally uninflated in *Chaetodipus*, and generally inflated in *Perognathus*, being as much so in some species as in *Cupidinimus* (see below, p. 127), though never reaching the extremes shown by *Dipodomys* and *Microdipodops*. The zygomatic process of the maxillary shows variable but slight amounts of inflation, paralleling *Cupidinimus*, but not as well developed.

P^4 consists of a curved metaloph of three cusps—the metacone, hypocone and entostyle—and a protoloph with a single cusp, the protocone. In almost every instance studied, the protoloph, on being worn, unites with the center of the metaloph—i.e., with the hypocone (fig. 3). In *P. flavus mesopolius* and to a lesser extent in *P. f. flavus*, however, the protoloph shows a tendency to move its point of union buccally, until it reaches the valley between the hypocone and the metacone (fig. 13). This is the manner in which the union is formed in *Microdipodops*, and appears, on first sight, likewise to be a plausible explanation of the manner in which the pattern found in *Dipodomys* has been attained. It is, however, only superficially similar, since, in the last genus, the metacone has moved forward, blocking the median valley, and usurping the rights of the hypocone, whereas in *P. flavus*, and apparently in *Microdipodops*, the change is brought about by the movement of the protocone. In most species, the premolar is narrower than the first molar, but in *P. l. longimembris*, the premolar is wider than any of the molars, a specialization in the same direction as occurs in *Microdipodops* (see fig. 30).

M^{1-3} have fundamentally the same pattern as in *Heliscomys gregoryi*, differing chiefly in the greater height of crown and more progressive lophization (fig. 3). Lakes may sometimes be formed on the crown, which, from their ephemeral nature, might be called playa lakes. As in *Perognathoides*, they are developed by the meeting of the bases of the paracone and metacone after the lophs have united lingually, but before the protocone and hypocone have fused. They are very minor features, instead of being major elements of the crown, as in the Heteromyinae, where, as pointed out below, they are formed by the union of the buccal margins of the paracone and metacone. The playa lakes are best shown in M$^{2-3}$ of *P. spinatus.* As in other genera, there appears to be no hypocone in M^3, although a sixth cusp sometimes occurs, at the buccal margin of the metaloph, as in *P. parvus.* This appears to have budded off from the metacone. Other modifications of the normal pattern occasionally occur. In *P. penicillatus pricei* and *P. flavus mexicanus,* an H-pattern is developed in the upper molars, due to the lophs first uniting between the protocone and the hypocone. This appears to be unique among the upper molars of heteromyids. Occasionally an anterior cingulum is developed on the molars, extending from the paracone to the protostyle, apparently an outgrowth from the latter. Sometimes an additional cuspule is developed at the center of this cingulum. This is shown, in an early stage of development, in *P. f. femoralis,* and, more firmly established, in *P. a. apache, P. longimembris brevinasus* and *P. m. merriami.*

P$_4$ normally has the normal Perognathine pattern, being a four-cusped tooth, whose cusps units in the center to form an X. This is well shown in *P. fallax* (fig. 2). One modification that is sometimes present is shown in fig. 14, where there is a postero-median cuspule, paralleling *Dipodomys.* In *P. spinatus* and *P. nelsoni,* there are a remarkable series of variations from normal. In *P. s. spinatus,* the union between the lophs, instead of being in the center of the tooth, has moved buccad, being between the lingual margins of the mesoconid and hypoconid (fig. 15). In *P. nelsoni,* this migration has proceeded


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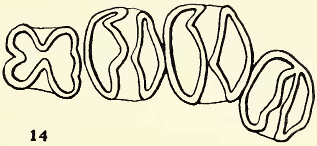
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FIG. 13. *Perognathus flavus mesopolius,* A. M. N. H. no. 68712, LP^4, × 10.
FIG. 14. *Perognathus hispidus paradoxus,* A. E. W. no. 1336-a, RP$_4$—M$_3$, × 10.
FIG. 15. *Perognathus s. spinatus,* A. M. N. H. no. 4567, RP$_4$, × 10.
FIG. 16. *P. n. nelsoni,* A. M. N. H. no. 21007, RP$_4$, × 10.
FIG. 17. *P. n. nelsoni,* A. M. N. H. no. 21011, RP$_4$, × 10.
FIG. 18. *P. spinatus nelsoni,* A. M. N. H. no. 31854, RP$_4$, × 10.
FIG. 19. *P. spinatus peninsulae,* A. M. N. H. no. 32345, RP$_4$, × 10.

further, and the lophs of the premolars unite first on the buccal side, as do the lophs of the molars. Stages in this modification, in which the two lophs have united before the cusps of the metalophid have done so, are shown in figs. 16-17. This process tends to bring the mesoconid and hypoconid close together, so that it is not surprising to find a further stage, represented by *P. spinatus nelsoni* (fig. 18), in which the tooth is but three cusped, the buccal cusps having fused, giving a pattern closely resembling that of *Heliscomys vetus* (fig. 7). This modification of the premolar is here treated as degeneration, the above stages being considered as steps in that direction, but the same series, if put in reverse order, could be interpreted as progressive specialization. However, as the Miocene forms already had four cusps, the long time gap since *H. vetus*, the last previous heteromyid with a three-cusped P_4, rules out this interpretation. The fact that M_1 shows a considerable increase of size in the species with three cusped premolars, and that P_4 shows a considerable number of other variations in these species, suggests that the premolar is losing its adaptive value, its functions being taken over by the molar, which would explain the opportunity for degeneration. It is possible that this three cusped pattern represents a reversion to the ancestral condition in one of the manners suggested by A. E. and H. E. Wood (1933). In *P. anthonyi* and *P. spinatus brevis*, the protoconid and mesaconid are very close together, as in *Proheteromys parvus* (fig. 5). An anteroconid, similar to that in *Liomys* and *Diprionomys*, occurs in *P. spinatus peninsulae* (fig. 19). In this race, the protoconid and mesoconid unite with each other, as well as through the anteroconid, thus surrounding a small enamel lake, paralleling *Liomys* and *Heteromys* (see figs. 130 and 139-140).

While these last forms mentioned verbally cross one of the limits established for the subfamilies, their significance is really of another sort. From the great range of variation in the pattern of P_4 in *P. spinatus*, it is obvious that something has happened in this species to upset the stability of the genes governing the premolar. It is particularly striking that, while some of the resulting phenotypes are like nothing noticed elsewhere, some are close parallels to, if not identical with, mutations occurring in other phyla of the same family, and, to a lesser extent, to ones occurring in the related family of Geomyidae. That is, similar genetic composition permits identical mutations, and the closer the genetic relationship, the greater will be the number of identical mutations. It is possible that the *P. spinatus* group represents an active stage of speciation.

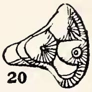
P. f. flavus and *P. p. pernix*, as well as *P. hispidus paradoxus* develop the postero-median cusp (fig. 14). *P. parvus* is characterized by the presence of a small hypostylid in almost every specimen, paralleling *Liomys* and *Heteromys* (fig. 138).

In M_{1-2}, the H-pattern, caused by the union of the lophs between the protoconid and hypoconid, becomes progressively developed (fig. 14). In some species, as *P. penicillatus pricei*, *P. fallax* and *P. longimembris brevinasus*, there appears to be no trace of this pattern. In others, as *P. nelsoni*, it appears briefly in some specimens but not in others. In *P. parvus* and *P. hispidus paradoxus*, it is well shown. In M_3, the hypolophid is sometimes two cusped, and sometimes three cusped, the two types appearing with about equal frequency, and apparently having little or no relationship to any other characters. In some forms, the lophs of M_3 unite first at the lingual margin, due to the absence or extremely poor development of the buccal cingulum in the posterior half of the tooth. If the hypostylid is present, the union is buccal. The H-pattern is never as well developed in *Perognathus* as it is in the lower molars of *Dipodomys* or *Microdipodops*.

The deciduous premolars show several stages which fill the sequence almost perfectly between the pattern found in the permanent premolars of *Perognathus* and the deciduous premolars of the other recent genera, which are all highly specialized. *P. apache* has the least specialized $dP\frac{4}{4}$ of any form studied (Tullberg, 1899, Pl. 27, figs. 27-28 shows this stage). The main cusps of dP^4 are as in P^4, but there is a cingulum running forward from the entostyle, around the front of the protocone, to the metacone (fig. 20). This specialization is almost identically that in the tooth figured by Wood (1932, fig. 29, see below, fig. 96) which thus seems very probably to be a deciduous premolar, referable to *Proheteromys magnus*. In other species of *Perognathus*, as *P. flavus bimaculatus*, a small cuspule has arisen anterior to the protocone, developed from the cingulum. A later stage, in which a cusp has arisen from the cingulum external to the protocone, and another from the lingual cingulum near the same cusp, is represented by *P. penicillatus pricei* (fig. 21). A somewhat different manner of development is shown in *P. m. merriami*, where these cusps do not show their cingular origin, but appear to be buds from the protocone, although this is probably an illusion. In *P.*

parvus (fig. 22), a final stage has been attained, with the formation of a metastyle, lateral to the metacone, and the complete lophization of the tooth, so that here are two multicusped lophs, with an anterior one of two cusps, apparently formed either by a splitting of the normal anterior cusp, unless the second one is an upgrowth from the base of the crown. This is, in fact, a further specialization than the basic pattern of the deciduous premolar of other heteromyids, the tooth of *P. penicillatus pricei* being a closer approach to the common stem.

In dP_4, there has been less variation. The most primitive pattern among the forms studied is again represented by *P. apache.* Here the pattern is dominated by four cusps which appear to be homologous with the four cusps of the permanent premolar (fig. 23). An anteroconid is present, analogous at least to the similarly placed cusp in P_4 of *Diprionomys* and *Liomys* (see below, figs. 103, 130). A posterior cingulum is present, from the buccal margin of which a small hypostylid is developing. Most of the other species show but little advance beyond this pattern, except in increasing the size of the two accessory cusps (see figs. 24-25). *P. hispidus paradoxus* (fig. 26) shows the greatest advance of any species studied, in the forward displacement of the anteroconid, approaching the conditions in other genera. In *P. h. hispidus*, the posterior cingulum gives rise to four small cuspules. The deciduous premolars are never worn smooth in *Perognathus* as they are in *Dipodomys* and *Heteromys*.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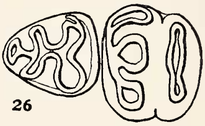
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FIG. 20. *Perognathus a. apache*, A. M. N. H. no. 6692, LdP^4, × 10.
FIG. 21. *P. penicillatus pricei*, A. M. N. H. no. 7148. LdP^4, × 10.
FIG. 22. *P. parvus*, A. M. N. H. no. 33535, LdP^4, × 10.
FIG. 23. *P. a. apache*, A. M. N. H. no. 6692, RdP_4, × 10.
FIG. 24. *P. penicillatus pricei*, A. M. N. H. no. 7148, RdP_4, × 10.
FIG. 25. *P. parvus*, A. M. N. H. no. 33535, RdP_4, × 10.
FIG. 26. *P. hispidus paradoxus*, A. E. W. no. 1336-b, RdP_4—M_1, × 10

The pits between M_3 and the base of the ascending ramus range from being entirely non-existent, as in *P. pernix*, *P. fasciatus* and *P. longimembris*, to being well developed, as in *P. flavus* and *P. baileyi rudinoris*. As there is never a foramen in the pit, the structure is closer to that of *Microdipodops* than to that of *Dipodomys*. The foramen is high on the side of the ascending ramus, with a canal running from it down the side of the bone, disappearing at the bottom of the pit, if one is present. In *P. fasciatus flavescens*, the wall of this canal is quite thick. In most of the other species, it is very thin, being easily broken through, as in *P. penicillatus eremicus* and *P. spinatus bryanti*. It appears likely that the foramen in the bottom of the pit in *Dipodomys* was originally high on the coronoid as in the other genera of the family, and that gradual thinning and elimination of the wall of the canal caused the migration of the foramen. The slope of the masseteric crest varies from about 45° as in *P. fallax* and *P. hispidus*, to essentially vertical at the anterior end, as in *P. penicillatus eremicus*, *P. f. fasciatus*, and *P. fasciatus flavescens*, a close similarity to *Microdipodops*.

The intermembral indices[3] in the two subgenera supply an interesting example of the well-known principle of lack of uniformity in rate of evolution of different structures. In the subgenus *Perognathus*, which approaches most closely to *Microdipodops* and *Dipodomys* in the skull characters, the intermembral indices are the largest, and hence the furthest from those of the saltatorial forms (see Table V).

The tail is tufted, as in *Dipodomys*. *P. flavus mesopolius* has an unusually long, strongly tufted tail. In *Microdipodops*, on the other hand, the tail is short and not tufted. There are no median ventral foramina in the caudal central of any specimens examined. The astragalus articulates with the cuboid, which sends a long process between the calcaneum and the navicular, to meet the astragalus. The dorsal surface of the ectocuneiform is hour-glass-shaped (see below, fig. 153).

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[3] The Intermembral Index is the ratio of the length of humerus + radius to femur + tibia, times 100, or $\frac{(R + H) \times 100}{T + F}$. The Revised Intermembral Index includes also the effective foot length, or distance from the center of the astragalus to the average of the ends of the three longest metatarsals, or $\frac{(R + H) \times 100}{T + F + P}$. (See Howell, 1932, pp. 521-522). These ratios, especially the second, give a very accurate measure of ricochetal ability, as they express the reduction of the fore limb in terms of the hind (See Table V).

The characters which appear to tend toward *Microdipodops* are not concentrated in one form, or in any one group, but are scattered indiscriminantly throughout the genus. This reduces the probability of *Perognathus* being ancestral to *Microdipodops*, as, if it were, it would be expected that the forms which were nearest the kangaroo mouse would have a larger number of characters in common with it than would those more distantly related. The actual distribution of common characters suggests that the genus *Perognathus* as a whole is evolving in such a manner as to parallel the saltatorial forms, some species developing one mutation identical to one in *Microdipodops*, and others another. This in itself argues close relationship between the two genera (Table I).

Perognathus is widely distributed throughout the more arid portions of temperate North America, extending from British Columbia to southern Mexico (see map, fig. 155). It frequents many varieties of environment, from lava fields to sand banks. All species are apparently primarily scamperers, but show an incipient progress toward saltation, as shown by their revised intermembral indices, ranging, in the specimens measured, from 47.7 to 52.5, with an average of 50.1 (see Table V). This conclusion is the same as that reached by Hatt (1932, p. 627), who says that *Perognathus* shows strong bipedal potentialities, but that it rarely, if ever, ricochets.

Perognathus furlongi Gazin, 1930

Fig. 27; Gazin, 1930, Pl. 3, figs. 5, 5a, and 6.

Holotype: C. I. T. Coll. V. P. No. 35, from the Upper Miocene Upper Cuyama Beds of Ventura County, California.

Diagnosis: Dorsal surface of muzzle broad with naso-frontal suture anterior to fronto-premaxillary suture; palate broad; diastema long; tooth row convex outward; teeth fairly low-crowned, characteristically Perognathine.

This species is a primitive species of *Perognathus*, differing from the later members of the genus, to which it could easily be ancestral, in the entire absence of any of the aberrant tooth specializations discussed above, and in the relatively low crowns of the cheek teeth (fig. 27).

The species differs from *Cupidinimus* in the absence of any tendency for the protoloph of P^4 to unite with the metacone. It differs from *Perognathoides* in the absence of additional cusps in the protoloph of P^4. Whether the incisors were grooved or not can not be told from

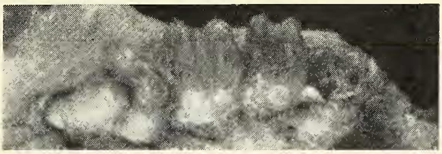


FIG. 27. *Perognathus furlongi*, Gazin, C. I. T. no. 35, LP^4—M^3, × 10. after Gazin, 1930.

Gazin's figures, but he has informed me that they are grooved. There was no indication of the connection between the protoloph and entostyle of P^4, which was already well developed in the slightly earlier *Peridiomys oregonensis.*

Thus there appears to be no evidence pointing toward the allocation of this species to any genus other than *Perognathus*, and considerable evidence, in the great similarity of tooth structure, indicating the correctness of such a determination. This unanimity of evidence is quite gratifying.

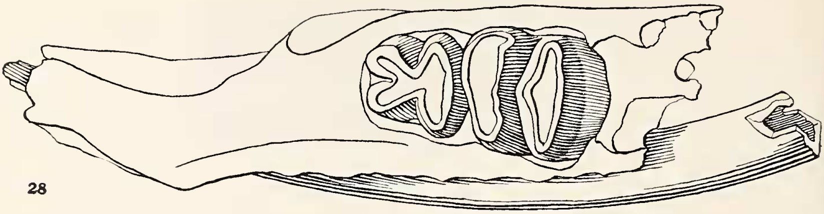
The relationships of this species to the later members of the genus are not certain at present, being separated from them by too long a time interval. It seems possible, however, that *P. furlongi* is ancestral to some or all of the later species. There is, at least, nothing in its known anatomy to prevent such an ancestral position, and it is so indicated on the chart (fig. 1). It is unfortunate that the auditory region is absent in this specimen. There is a slight advance represented in the teeth over *Mookomys altifluminis*, but the gap is slight, and the species could almost equally readily be referred to that genus.

P. coquorum n. sp. (Figs. 28-29.)

Holotype: H. J. C. No. 702, collected by Mr. H. J. Cook, Pliohippus Draw, Upper Snake Creek Beds, Pliocene of Sioux County, Nebraska.

Diagnosis: Size very large; cusps of protolophid of P$_4$ unusually distinct; teeth low-crowned.

P$_4$ is larger in comparison with M$_1$ than in *P. hispidus paradoxus.* The protoconid and mesoconid unite less with each other than in the recent form, and more with the metalophid, the valley between the two anterior cusps being unusually well developed (fig. 28). These are primitive characters, as would be expected in the early members of the genus. In M$_1$, the hypoconid projects well forward into the median valley, which is the initial step in the development of the



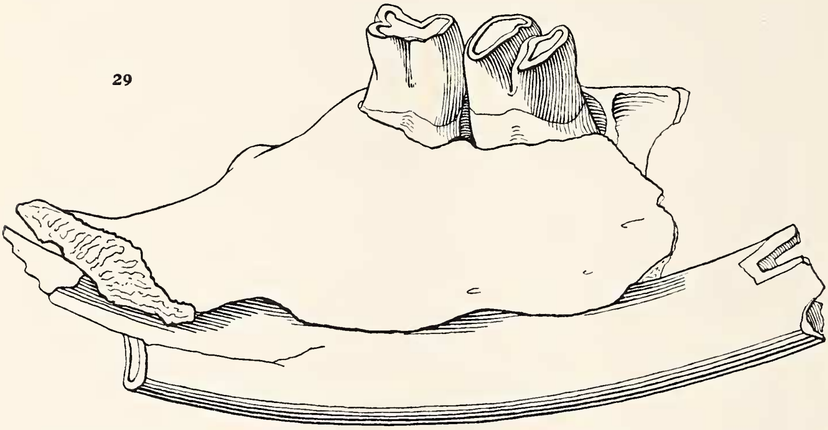


FIG. 28. *Perognathus coquorum*, H. J. C. no. 702, RP_4—M_1, × 10.
FIG. 29. *Perognathus coquorum*, H. J. C. no. 702, RP_4—M_1, × 10.

H-pattern (fig. 14). The diastema is long, 25% longer than that in *P. h. paradoxus*, the largest (fide Osgood, 1900) of the modern species of the genus.

The large size, relatively low crowns, and the primitive character of P_4 are the most important known characters of this species. If the size is of great phylogenetic significance, it would rule this species out from possible ancestry to the later and smaller species of *Perognathus*. But as I consider size of relatively minor importance, and as this species otherwise appears to be primitive, and as it is probable on other grounds that the smallest living species, at least, of *Perognathus* are reduced in size, I have not hesitated to place this species in an ancestral position on the chart (fig. 1).

I take great pleasure in naming this species after the whole family of Cooks, in grateful appreciation of the kind hospitality they have always shown me on my visits to Agate, and as a partial recognition of the debt owed to them by vertebrate paleontology in general and by me in particular.

Perognathus sp. indet.

A. M. N. H. No. 27791, collected by J. W. Gidley, in 1924, from the Upper Pliocene Curtis formation, near Benson, Arizona.

As none of the cheek teeth are preserved in this specimen, and the alveoli for the last two molars are poorly preserved, very little can be told of its affinities. It is a heteromyid, whose small size appears to warrant its inclusion in *Perognathus* or some similar genus, and its late horizon increases the probability of its reference to *Perognathus* being correct (Table II). It is perhaps related to *P. parvus* or some of the other small recent species. If it is descended from any known Miocene or Pliocene form, it represents a case of evolutionary modification with reduction of size, and thus, presumably, would count as a case of reversed evolution.

Specimens of *Perognathus* are known from the Pleistocene of Rancho La Brea, which Dice (1925) refers to *P. californicus californicus*, and which he says show no difference from living members of the same subspecies.

Heteromyids occur in, but have not as yet been described from, the Pleistocene of Nebraska.

Microdipodops Merriam, 1891

Figs. 30-33; Howell, 1932, figs. 21-M, and 23-M.

Genotype: M. megacephalus Merriam, 1891, from Nevada.

Diagnosis: Skull more highly inflated than in any other heteromyid; anterior lip of auditory meatus expanded until it passes ahead of the glenoid; lateral borders of parietals excavated to receive squamosals; P_4 sextitubercular or pentatubercular with X-pattern, the additional cusps being derived from an external cingulum; H-pattern well developed in lower molars; $M\frac{3}{3}$ much reduced; upper molars form enamel lakes by surrounding median valley, as in *Liomys;* P^4 as in *Perognathus;* cheek teeth extremely high crowned, but apparently not ever-growing; zygomatic process of maxilla not expanded as in *Dipodomys;* bullae reach below level of grinding surface of cheek teeth; enamel complete on all cheek teeth; no median ventral foramina in caudal vertebrae; tail not tufted; locomotion highly ricochetal.

Range: Recent of Nevada, California and Oregon (see map, fig. 155).

This genus combines the characters of diverse groups of heteromyids in a most remarkable manner. Many of the resemblances to *Dipo-*

TABLE I. COMPARISON OF MICRODIPODOPS WITH CERTAIN HETEROMYIDAE AND DIPODIDAE.

The Dipodid is included to give an indication of which features are ricochetal habitus characters, as there is no relationship between the Heteromyidae and Dipodidae, but similar body-forms.

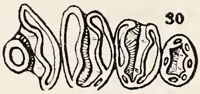
Microdipodops	Perognathus	Dipodomys	Heteromys	Liomys	Jaculus
Locomotion richochetal	....	×	....	....	×
H-pattern in lower molars	×	×	....	....	....
X-pattern in lower premolar	×	×	....	....	....
$M\frac{3}{3}$ reduced in size	×	×	....	....	....
Protoloph of P^4 unites between hypocone and metacone	×	....	....	....	....
Protoloph of P^4 one cusp	×	?	....	....	....
Upper molars surround central lakes	....	....	×	×	....
Playa lake in metaloph of P^4	....	....	×	×	....
Cheek teeth hypsodont	....	×	×	....	....
Pattern not elongated with crown	....	×	....	....	....
Teeth rooted	×	....	×	×	×
Upper incisors grooved	×	×	....	....	×
Bases of upper molars not in orbit	×	....	×	×	×
Zygomatic process of Mx. unexpanded	×	....	×	×	....
End of palate behind M^3	×	....	×	×	×
Pits in basioccipital	....	....	×	×	×
One pair of pterygoid fossae	×	....	....	....	×
Pterygoid fossae reach endocranium	×	....	....	....	....
Masseter separated from IOF by crest	....	....	....	....	....
Orbit not overhung by frontal	×	....	×	×	×
Ethmoid foramen present	×	....	×	×	....
Incipient post-orbital process	....	....	....	....	×
Distinct temporal fossa	....	....	×	×	×
Alisphenoid canal antero-dorsad	×	....	....	....	....
Bulla extends anterad of glenoid	....	....	....	....	....
Three-chambered bulla	×	×	....	....	×
Squamosal perforated by bulla	....	×	....	....	....
Lacrymal not expanded, free of Mx.	×	....	×	×	....
Parietal between squamosal and mastoid	×	....	....	....	×
Interparietal often paired	....	....	....	×	....
Paroccipital process latero-caudad	....	....	×	×	....
Masseteric crest steep, with knob	×	×	....	....	....
Knob for pulp cavity at lower edge of ascending ramus	....	....	....	....	×
No pit by M_3, foramen on condyloid	×	....	×	×	....
Cervical vertebrae fused in part	....	×	....	....	×
No median ventral foramen in caudals	×	....	....	....	....
Notch in transverse process of caudals gently curved	....	×	....	....	....
Tail not tufted	....	....	×	×	....
Scapula prolonged posteriorly	....	×	....	....	....
End of acromion expanded	....	....	×	×	×
Short supinator crest	....	×	....	....	×
Deltoid crest ends steeply	....	×	....	....	×
Articulation of trapezium and scapholunar	....	×	....	....	×
Manus long and slender	....	....	....	....	....
Gluteal fossa larger than iliac	×	....	×	×	....
Triangular obturator foramen	....	×	....	....	....
Process of pubis at front of obturator foramen	....	×	....	....	....
Symphysis pubis very short	....	....	×	....	....
Cnemial crest ends at gentle slope	×	....	×	×	....
External and internal malleoli reach same level	....	....	×	×	×
Astragalo-cuboid contact	×	....	×	×	....
Hour-glass-shaped ectocuneiform	×	×	....	....	....
Metatarsal IV the longest	....	....	×	×	....

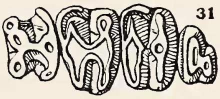
domys (Table I) are obviously correlated with its ricochetal habitus, and are not necessarily significant of close relationships. The foot structure seems indicative of relationships with *Perognathus*, on the basis of the astragalo-cuboid contact and the hour-glass-shaped ectocuneiform. There are several characters which seem to indicate Heteromyine affinities, as well as some which are distinctive. But the largest number of significant resemblances appear to be to *Perognathus*. Of the characters allying *Microdipodops* with *Dipodomys*, all but two (the transverse processes of the caudal vertebrae and the process of the pubis at the anterior end of the obturator foramen) are either obviously habitus characters, or else are shared with *Perognathus*, too. If this genus is not a Perognathine, it may represent an independent line, to be defined as a fourth subfamily, or it may be an aberrant Heteromyine. For the present, it seems best to include it among the Perognathinae (fig. 1).

The cheek teeth are very high crowned, the roots not developing until the crown has reached a height two or three times that in *Perognathus*. As I did not have an opportunity to study a large series of specimens, the individuals in which roots were seen in an early stage of development may be aberrant. Merriam (1891) states that the teeth are rootless. The fact that he studied *M. megacephalus* and that included in the present paper is from California, presumably *M. californicus*, may account for the difference. It does not seem likely that roots are present in the young, and absent in the adult, animals. The roots, if regularly present, are certainly greatly reduced in size.

The protoloph of P^4 appears unicuspidate. Apparently it unites with the metaloph in the space between the metacone and hypocone, being thus very suggestive of P^4 of *Perognathus flavus* (fig. 13), and representing a parallel method of development to that shown in P^4 of *Dipodomys*. The tooth retains its two-lophed character for a long time, perhaps throughout life. The metaloph of P^4 is the widest part of the upper series (fig. 30). In entirely unworn teeth, there is a cingulum on the posterior side of the tooth, with an incipient cuspule, behind the hypocone, from which a playa lake might develop on wear, although it is not certain that one would be formed.

In M^{1-2} the lophs unite first at the lingual side, and apparently make their next point of union at the buccal margin (fig. 30). The central lake of enamel so developed would be short-lived, though not as transient as the lake on the premolar. No specimens with this lake





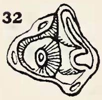


FIG. 30. *Microdipodops californicus*, U. Cal. no. 48660, LP^4—M^3, × 10.
FIG. 31. *M. californicus*, U. Cal. no. 48660, RP_4—M_3, × 10.
FIG. 32. *M. californicus*, U. Cal. no. 38670, LdP^4, × 10.
FIG. 33. *M. californicus*, U. Cal. no. 38670, RdP_4, × 10.

were seen, but from the unworn teeth it appears certain that such would develop. This is an important resemblance to *Liomys* and *Heteromys*. The very short life of these lakes is due to the extreme shortening of the occlusal part of the crown, while the alveolar part, beyond the limits of the valleys, becomes greatly elongate. In this respect, *Microdipodops* strongly suggests *Dipodomys*, and equally markedly differs from *Liomys* and *Heteromys*, in which the whole crown is elongated at an equal rate. M^3 is much reduced, making it difficult to determine the elements of the pattern even in an entirely unworn tooth, but careful study reveals six cusps, the usual three in the protoloph, and an entostyle, metacone and a sixth buccad of the metacone, similar to the cusp in this position in *Perognathus parvus*, except that it is extremely large.

P_4 and M_3 are proportionately larger than in *Perognathus*, though smaller than the first two molars (fig. 31). P_4 is six cusped in some specimens and five cusped in others, the difference being in the presence or absence of a buccal cusp of the protolophid, which apparently is derived, when present, from an external cingulum. If this interpretation is correct, the buccal cusp of the metalophid is probably also of cingular origin, and the union of the two lophs would very definitely be between the mesoconid and hypoconid, differing from the normal X-pattern of *Perognathus*, but suggestive of the modified pattern in *P. nelsoni* (figs. 16-17). In P_4, the mesostylid, when present, is antero-external to the mesoconid. M_{1-3} have well-developed

H-patterns, suggesting *Dipodomys*. In M_3 there is a strong cingulum covering the whole anterior face of the tooth, and the three-cusped hypolophid is reduced, though not to the degree to which it has been in *Dipodomys*. The protostylids of M_{1-2} send cingula along the anterior face of the protoconids. This again is a similarity to the conditions found among the Heteromyinae. The cingula of the lower molars, together with the other Heteromyine features mentioned, suggest that *Microdipodops* belongs to that subfamily, but the reduction of the pattern-bearing portion of the tooth has proceeded to such a stage as to conceal and largely to obliterate the proofs of the real relationships. The similarities to the Heteromyinae are more probably, however, merely another case of the parallelism so abundant among rodents in general and heteromyids in particular.

The upper milk molar (fig. 32) is close to the corresponding tooth of *Perognathus penicillatus pricei*, consisting of three crests, although the buccal cuspule of the metaloph is not as well developed as in the latter species. The rest of the loph is clearly three cusped, the lingual cusp being obviously of cingular origin. The protoloph is two cusped, the buccal cone appearing to be a protostyle. The most anterior crest is subdivided into two cusps, the lingual one developing as a spur from a discontinuous internal cingulum.

The lower deciduous premolar (fig. 33) shows greater advance over that of *Perognathus* than does the upper. The metalophid is three cusped, with a broad posterior cingulum. In some specimens, a cusp seems to have been formed from the middle of this cingulum. The protolophid is likewise three cusped, the mesostylid being fairly small. The four primary cusps unite in an X-pattern. The anteroconid of dP_4 of *Perognathus* appears to have moved forward. As it moved, the crest by which it was united with the primary cusps was carried with it, forming a ridge from the protolophid to the anterior edge of the tooth. As the cusp moved forward, the cingulum to which it was united, and from which it may have arisen, moved with it, retaining its connections at both ends with the protolophid. At the same time, two cusps arose from the buccal part of the cingulum, forcing the already-existing stylid to the lingual margin of the crown. This process is superficially the same as that by which the corresponding teeth were developed in *Dipodomys* and *Heteromys*, but appears to have followed a slightly different method of development.

In *Perognathus*, the upper deciduous premolar showed considerable progressive specialization, but the lower one appeared to have remained in a fairly primitive condition. In *Microdipodops*, the upper remained essentially as in *Perognathus*, but the lower has advanced considerably, bringing the patterns in both teeth into line with those found in the other subfamilies.

The grooving of the incisors in *Microdipodops* is as in *Perognathus*, *Dipodomys*, and other genera. In all specimens of *Microdipodops* studied, the enamel of the incisors was very pale yellow. The same feature was found in young specimens of *Perognathus* and *Dipodomys*, and probably merely represents a juvenile character.

The most striking feature of the skull of *Microdipodops* is the tremendous inflation of the bullae, surpassing even that which occurs in *Dipodomys deserti* (Howell, 1932, figs. 21, 23). The inflation has affected both skulls in much the same manner, that is, it results in the crowding of the parietals, interparietal and occipitals. In *Microdipodops*, as in *D. deserti*, the bullae meet above the interparietal, as well as below the basisphenoid. The bulla in *Microdipodops* has an additional lobe, formed by the swelling of the anterior lip of the external auditory meatus, which reaches forward, in this genus, until it extends nearly half the length of the zygoma, and passes the frontoparietal suture.

The nasals are produced far in front of the incisors. There is a well marked, though slight, crest separating the fossa for the masseter from the infraorbital foramen, as well marked, however, as in the smaller genera of sciurids. As in *Perognathus*, the lacrymal is separate from the maxillary, and is unexpanded. This is chiefly due to the lack of expansion of the zygomatic process of the maxillary, which, in *Dipodomys*, reaches to and unites with the lacrymal. The squamosal is carried up onto the dorsum of the skull, forming a deep notch in the parietal. This notch is the temporal fossa, the temporalis apparently having migrated and carried the squamosal with it. This is suggestive of *Heteromys*, where the temporal fossa likewise is considerably expanded, and has carried the squamosal with it. The parietal does not reach this fossa for the temporalis. Just anterior to the notch is a small process, formed of the frontal and squamosal, which suggests an incipient post-orbital process, and is of interest as indicating a method by which the post-orbital process of the Sciuridae may have originated. An arm of the parietal extends for some distance along the rear of the orbit-temporal fossa, separating the squamosal and mastoid for about half the length of the former. On the rear wall of the temporal fossa is a perforation, allowing the bulla to show through into the fossa—a condition sometimes met with in *Dipodomys*, but apparently always present in *Microdipodops*. The anterior end of the alisphenoid canal is higher than in either *Dipodomys* or *Heteromys*, giving the canal a dorsal inclination, as in *Perognathus*. It further differs from *Dipodomys* in that its anterior end is in the center of the alisphenoid, not at the anterior edge. The malar is less reduced than in *Dipodomys*. A slender bar from the dorsal margin of the alisphenoid makes a contact with the bulla —a condition not seen in any other genus, though approached in *Perognathus parvus*. The basioccipital resembles that of *Heteromys* more nearly than any other form in the deep pits on its ventral surface for the longus capitis muscle. The basioccipital does not decrease uniformly in diameter from rear to front, but makes a temporary halt at about its center.

The two bullae meet ventrad of the basisphenoid, and do not squeeze it between them, as is the case in *Dipodomys*, and, to a lesser degree, in *Perognathus*. In *Dipodomys*, the basisphenoid is reduced to a thin thread. The pterygoids are nearest in shape to those of *Perognathus*. A foramen is present near the dorsal margin of the orbit, apparently the ethmoid, as in *Perognathus*, *Liomys* and *Heteromys*, which is not found in *Dipodomys*. The pterygoid fossae resemble those of *Perognathus* in the uninterrupted nature of their continuation into the endocranial regions. In this they are widely removed from *Heteromys*, in which the dorsal side of the fossae is not perforated at all. The paroccipital processes extend caudad and laterad but not ventrad, thus resembling *Heteromys* and differing from *Dipodomys* and *Perognathus*. In *Perognathus* and *Microdipodops*, there are only one prominent pair of pterygoid fossae, the anterior pair of other forms being almost invisible. In *Dipodomys*, the anterior pair are of medium size, and in *Heteromys*, they are as large as the posterior one. The skull index (see above, p. 97, footnote) is 68.8.

In the mandible, the masseteric crest ends anteriorly much more vertically than does that of *Perognathus*, and has a large knob at the anterior end, just below P_4, some distance from the mental foramen. A foramen is present at the base of the coronoid process as in *Dipodomys*, though not as far forward as in that genus, nor is it in a pit. The foramen is below the junction of the coronoid and condyloid processes, and not posterior to the junction, as in *Perognathus* and *Heteromys*. The foramen, however, is no closer to its position in *Dipodomys* than to that in *Perognathus*. The general size and shape of the angle seems to be closest to that of *Liomys* and *Perognathus*. The knob marking the pulp cavity of the incisor is at the lower edge of the ascending ramus, instead of at its center, or upper side, as in the other genera. The small size of the knob is a closer approach to *Heteromys* than to any of the other genera, although the small size in *Microdipodops* may be due to the fact that all the specimens studied were immature animals. One of them, however, appears to be nearly adult, and is the only specimen in which any trace at all of the knobs could be discovered. The jaw is very small and slender, and the symphysis short.

The vertebrae have been carefully studied by Hatt (1932), and very little can be added to his work. In the caudals, there seems to be no median ventral foramen, thus resembling *Perognathus*. The transverse processes of the caudals are deeply notched in the center by a wide U-valley, as in *Dipodomys* and *Diprionomys*, instead of being cut by a sharp V-valley as in *Perognathus*.

The posterior prolongation of the scapula is very suggestive of that of *Dipodomys*. The metacromion is very small, but nevertheless larger than in either *Perognathus* or *Dipodomys*. The free end of the acromion is not expanded as it is in *Perognathus* and *Dipodomys*, in which it approaches *Heteromys*.

The humerus is much like that of *Dipodomys*. The supinator crest is shorter in *Microdipodops* than in *Dipodomys*, and shorter in the latter than in any other members of the family. The greatly enlarged deltoid process has reached one stage beyond that found in *Dipodomys*, ending in a strong expansion, and with a distal slope at 90° to the shaft of the humerus. The entepicondyle is shorter than in *Perognathus*, larger than in *Heteromys*, and essentially as in *Dipodomys*. It is nearly as long in *Heteromys* as in *Microdipodops*, but not so wide. The sharp proximal end of the supinator crest distinguishes it from any other genus. The shaft of the humerus is definitely a larger part of the bone in *Heteromys* than in any other genus.

The carpus is nearly the same in all forms studied. The centrale of *Microdipodops* is proportionately much smaller than in any other heteromyid (fig. 152). The trapezoid articulates with the scapholunar as in *Dipodomys*, differing from *Perognathus* and *Cupidinimus*, in which there is no such articulation. The manus is long and slender in *Microdipodops*, differing in this from all other genera. The claws, though slender, are extremely long and powerful.

The obturator foramen is much wider dorso-ventrally in *Perognathus* than in any of the other genera, and more nearly round. In *Microdipodops*, it is subtriangular, and much compressed dorso-ventrally. *Dipodomys* and *Heteromys* are intermediate, the former being the nearer to *Microdipodops*. The symphysis is shorter than in any other form, *Heteromys* being the nearest approach. Correlated with the dorso-ventral compression of the obturator foramen, the pubis becomes more nearly parallel with the ischium than in any other member of the family. There is a slight posterior projection of the ischium, as in *Dipodomys*. As in this last form, there is a small process of the pubis near the anterior end of the obturator foramen to which a ligament is attached, separating a small anterior section of the foramen from a large posterior one. The gluteal fossa of the ilium is much larger than the iliac, as in *Heteromys* and *Perognathus*.

The shaft of the femur is straighter than in *Perognathus* and *Dipodomys*, and almost as straight as in *Heteromys*, being essentially like that of *Cupidinimus* (fig. 61).

The fusion of the tibia and fibula has proceeded further than in any other heteromyid, the fused portion being 59.4% of the length of the whole (see Table V). The cnemial crest ends gently instead of at a sharp angle as in *Dipodomys*. In this respect, it is closest to *Perognathus*, though not dissimilar to *Heteromys*. The groove separating the fibular and tibial parts of the bone at the distal end of the anterior surface is long and undercut, as in *Heteromys* and *Perognathus*. In *Perognathus*, the external malleolus extends distad of the internal; in *Dipodomys*, it extends very slightly distad; in *Microdipodops*, they are almost the same length; and in *Heteromys* they appear equal. The postero-median process of the tibia is short and curved as in *Perognathus*, *Dipodomys* and *Diprionomys*. The fossa is rather elongate, being intermediate between the conditions found in *Diprionomys* and *Heteromys* on the one hand, and those of *Perognathus* and *Dipodomys* on the other.

The tarsus is much like that of *Perognathus*, and constitutes one of the strongest arguments for its inclusion among the Perognathinae (see fig. 153). The cuboid-astragalar contact is well shown, the cuboid, as usual among the heteromyids, sending a long process between the navicular and calcaneum. A broad naviculo-calcaneal contact is developed in *Dipodomys*. The fact that it is also clearly shown in *Alactaga* and *Scirtopoda*, two of the jerboas (Howell, fig. 28, p. 529), would suggest that it is correlated with the ricochetal habitus, except for its entire absence in *Microdipodops*. The ectocuneiform has the hour-glass shape of that of *Perognathus* and *Dipodomys*, differing clearly from the parallel-sided bone of *Heteromys*. As in most genera, the mesocuneiform is much smaller than the ectocuneiform. Metatarsal IV is longer than III, a character elsewhere noted only in *Heteromys* and *Liomys*. The whole pes is long and slender. The distal ends of digits II-IV converge as in all truly ricochetal forms.

The revised intermembral index[4] is 41.8 (see Table V). The tibiofibula is extremely elongated, being about half as long again as is the femur.

Of all the forms studied, the nearest structural approach to *Microdipodops* is found in *Perognathus parvus*. It is possible that the kangaroo mice are descended from Miocene members of the genus *Perognathus*, but there is no direct evidence, and the results of these studies on the Heteromyidae have given me such a feeling of respect for the abilities of these rodents in imitating the developments of their relatives that I have considered it best to indicate this genus as a separate derivative of the Oligocene heteromyid stock, close to *Perognathus*, but with the intermediate stages unknown (fig. 1). If *Microdipodops* should be more closely related to *Perognathus* than is here considered to be the case, there seems to be little doubt that it is nearer *P. parvus* than to any other species which has been included in this study. It may, however, prove to be a highly modified Heteromyine.

Microdipodops occurs in portions of Nevada and adjacent areas of California and Oregon, which, in itself, suggests affinities with the Perognathinae rather than with the Heteromyinae, since the latter are at present entirely limited (other than *Microdipodops*) to Central and South America, (see maps, figs. 155, 157). *Microdipodops* appears to be much more restricted in its range than are the other members of the family, being found only in areas of vegetated fine sand (Hatt, 1932, p. 624; Hall and Linsdale, 1929, p. 299). There is probably some significance, from the phylogenetic view-point, in the

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[4] See Note 3, page 103.

restriction of the genus to the single type of habitat, and in the limited number of species referable to the genus. Does the limited distribution mean that the genus is just beginning its development, and has not spread far? Or does it mean that the form is on the down-grade, and has become limited to this one type of environment? Are there few species because the environment is restricted, or is the environment restricted because there are but few species? (For a consideration of some aspects of these problems, see Willis, 1922).

Subfamily Dipodomyinae Coues 1875 (1875*b*)

Premolars and molars as in Perognathinae, except that H-pattern is always present; cheek teeth progressively hypsodont, in *Dipodomys* becoming evergrowing; enamel progressively interrupted, eventually reduced to anterior and posterior plates; M^3_3 reduced in size; increase in height of crown does not affect the pattern, which is rapidly destroyed, leaving only an enamel oval; P_4 never more than five-cusped, the fifth appearing in the center of the metalophid; upper incisor smooth or grooved, the groove being deep when present; progressive expansion of the bullae and increase in richochetal ability; bullae rarely reach level of grinding surface of cheek teeth, and never extend appreciably below it; no ethmoid foramen in frontal; zygomatic root of maxillary progressively expanded antero-posteriorly; center of palate between premolars ridged; pterygoid fossae double; caudal vertebrae have median ventral foramina; calcaneal-navicular or even calcaneal-cuneiform articulation; tail tufted.

Genera: *Cupidinimus* and *Dipodomys*.

Distribution: Lower Pliocene of Nebraska; Middle Pliocene of Nevada; Upper Pliocene of Arizona; Pleistocene of California; Recent of western United States and Mexico (see map, fig. 156).

This subfamily is definitely related to the Perognathinae, to which it shows much closer relationships than does either to the Heteromyinae (fig. 1). It may be that a more correct idea of the relationships within the family would be attained by consolidating these first two subfamilies. But there is a very distinct difference in foot structure, together with other less noticeable differences. Therefore, it is considered best to separate the Dipodomyinae, though it is realized that they are close to the Perognathinae.

Cupidinimus new genus[5]

Genotype: *C. nebraskensis*, n.sp., described below, from the lowest Pliocene Valentine beds of Nebraska.

Diagnosis: Sub-ricochetal heteromyids, with asulcate upper incisors; union of lophs of P^4 tending to be between metacone and protoloph, though first point of union is usually in the center of the tooth; lower molars with incipient H-pattern; cheek teeth progressively hypsodont and lophate, but always rooted; deciduous premolars progressive; calcaneal-navicular articulation.

Range: Valentine (lowest Pliocene) of Nebraska, Thousand Creek (Middle Pliocene) of Nevada, and Benson (Upper Pliocene) of Arizona.

This genus is close to *Perognathus* and *Mookomys* in many respects, but in many more it shows fundamental similarities to *Dipodomys*, as will be shown below, and seems to be an ideal structural ancestor to that genus. There are no characters of *Cupidinimus* so far known that stand in the way of its ancestry to *Dipodomys*. The philosophy of evolution which would prohibit its derivation from *Mookomys*, because of the grooved incisors in the latter genus, would require a separate line leading back at least to the Lower Miocene. The structure of the teeth of this genus is quite different from that of *Perognathoides*. The remarkable character of the tarsus is less well established in *Cupidinimus* than it is in *Dipodomys*, so it is possible that *Mookomys*, in which the tarsus is of a more normal heteromyid type, may represent the point of divergence of the Dipodomyinae from the Perognathinae (see fig. 1).

Cupidinimus nebraskensis n. sp. (Figs. 34-65.)

Holotype: Carn. Mus. No. 10193.

Paratypes: C. M. Nos. 10170, 10171, 10172, 10173, 10174, and 10175.

Collected by A. E., F. D., and H. E. Wood, F. J. Johnson and C. S. Osborne, from the Valentine Formation, about three miles south of Valentine, Nebraska, July 15-16, 1931; Sept. 7, 1931 and Sept. 3, 1932.

Diagnosis: Small; teeth medium to low crowned; lophs separate until the teeth are much worn; masseteric ridge extends well forward of P_4; limbs definitely sub-ricochetal; calcaneal-navicular contact definitely established.

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[5] The name of this genus is intended to suggest the formation and locality where the genotype was found.

This species is known only from the lowest Pliocene of its type locality. Specimens occur in several isolated patches within a quarter of a mile of each other, and apparently at the same stratigraphic level (see map, fig. 34). The teeth are definitely more primitive than in *C. magnus*, the only other species referred to the genus. The auditory region is somewhat specialized, but whether more so than in *C. magnus* can not be determined until a skull of the latter is found. The more primitive character of *C. nebraskensis* is no more than would be expected on the basis of the respective horizons of the two species.

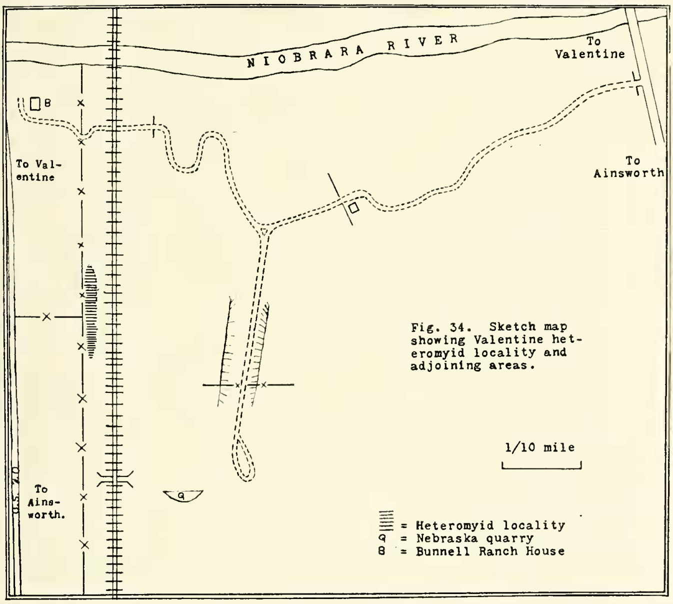

Fig. 34. Sketch map showing Valentine heteromyid locality and adjoining areas.

In June, 1931, a field party, consisting of Miss Rolena Dowden, Dr. Florence Dowden Wood, Dr. H. E. Wood and the author, had the good fortune to find considerable quantities of heteromyid bones, including a rather complete associated skeleton (fig. 35), as well as numerous other teeth and bones, in the Lower Pliocene Valentine beds of north-central Nebraska. During a visit, largely with the idea of learning as much as possible of the occurrence, to a field party of the University of Nebraska, who were working a quarry in the Valentine (see map), Messrs. C. S. Osborne and F. J. Johnson of the Nebraska party very kindly pointed out exposures in the neighborhood where

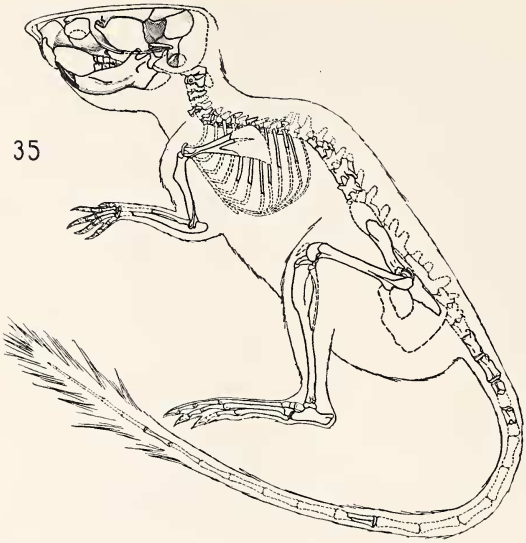

Fig. 35. *Cupidinimus nebraskensis*, holotype, C. M. no. 10193, Restored Skeleton. × 1.

they were not expecting to work. It was in one of these that the heteromyids were discovered.

This locality is on the opposite (west) side of the railroad embankment from the Nebraska quarry, in the sand flat just inside the fence at the edge of the railroad property, and about half way between the Nebraska quarry and the Bunnell ranch house. The fossils were scattered generally over the whole area, where it was not covered with grass, and were recovered by crawling over the ground on hands and knees, or, even better, by lying flat on the sand. Another visit was paid to the same locality on Sept. 7, the same summer, and a third visit was made on Sept. 3, 1932. On each of these visits, more heteromyid material was found, though on neither occasion was as much collected as on the first trip. As this pocket is extremely limited in area, having been covered thoroughly, without difficulty, on each visit, it would appear to be extremely rich in heteromyids. In the visit in 1932, as the Nebraska party was through working the quarry, we searched the refuse pile of the quarry, finding a few specimens of the same species, indicating that the two areas are of essentially the same age, and proving that the heteromyids are genuinely associated with the rest of the fauna.

The upper incisors are entirely without sulci in this species. A large collection of incisors was made in the sand flat, of appropriate size to belong to this species, not one of which shows the slightest trace of grooving. As not more than one or two specimens of any other species of small rodent was found, it is very probable that most of the incisors belong to this species. In the skull described below, the incisors were preserved, and are without sulci. The upper incisors, as always in rodents, have a lesser radius of curvature than do the lowers, the figures in this case being 4.4 mm. and 7.5 mm. respectively.

The upper premolar (figs. 36 and 37) is of the typical perognathine type, composed of two transverse lophs. The anterior of these is formed of a single cusp, apparently the protocone. The paracone seems to be absent in this as in all members of the Perognathinae and Dipodomyinae. The posterior loph is formed of the metacone, hypocone and entostyle. There is not as long an anterior slope of the protocone as in *Perognathus*, nor is it even as well developed as in *C. magnus*, though it is of appreciable size. This is a primitive character, correlated with low crowns. The union between the two lophs, as the crown is worn away, first develops at the buccal margin of the tooth, between the protocone and the metacone. The union between the two lophs does not take place, however, until the tooth is well worn, and is not shown in either specimen figured. The cusps of the metaloph unite with each other early in life. The metacone and entostyle are distinctly anterior to the hypocone, making the metaloph markedly crescentic, and partly blocking the median valley at both ends. As the tooth is worn, the hypocone extends further forward, approaching closer and closer to the protocone, uniting with it shortly after the metacone does, clearly indicating the manner in which the Dipodomyine method of premolar formation has been acquired. In this form, there is no trace of the buccal movement of the protocone, which occurs in *Microdipodops*, but rather the metacone has moved forward until it makes contact with the protocone. The posterior loph of the premolar is the widest part of the upper cheek tooth series, suggesting *Microdipodops* rather than *Dipodomys*.

M^{1-2} are each composed of two lophs, and contain six cusps each, as in all heteromyids, the two lophs of each being subequal in size, M^1 is definitely larger than M^2 (fig. 37). Wear affects the upper molars progressively from rear to front; that is, M^3 is the first worn to a circle, while M^1 is the last. This is the same situation that exists in *Pero-*

gnathus, *Microdipodops* and *Dipodomys*. The paracone and metacone have unusually acute external margins. In another specimen, C. M. No. 10175, M^1 is but slightly worn, and the outlines of the individual cusps can still be easily seen on the lophs. The two lophs are still separate, but are almost ready to unite at the lingual margin. The valley between the four primary cusps is still quite deep. In this animal, the two cingular cusps unite with each other earlier than they do in *Perognathus*, as compared with the time when the other portions of the lophs unite with each other. Or perhaps it might be put this way—the gradient of the median valley is much steeper in *Cupidinimus* than it is in *Perognathus*.

M^3 is much smaller than are the other teeth (figs. 37-38). The anterior loph is composed of three cusps, as in the other molars, but the metaloph contains only two, the metacone and a cusp of somewhat problematical homologies. Comparison with *Heliscomys gregoryi* suggests that it may have been derived from the cingulum and thus be homologous with the entostyles of the other teeth. It may have resulted from a splitting of the metacone, but the former seems definitely the more probable. As no hypocone appears to be present, or ever to have been present, it may be that this cusp should be considered as a cingulum hypocone. The protostyle is quite small and shows (fig. 38) what appears to be an incipient anterior cingulum, apparently the initial step in the development of the very strong cingulum shown in the unworn third upper molar of *Microdipodops* and *Dipodomys*.

The lower premolar (fig. 39) has a typical X-pattern, being comcomposed of four cusps, uniting in the center of the tooth. The premolar is smaller than the first two molars, a primitive character, though it is not reduced, as in *Perognathus*. The four cusps are much more independent of each other than in the recent species of pocket mice, the union of the two lophs, especially, being less well developed. The general effect, however, is similar to that in the Tertiary species of *Perognathus*. In these characters, this form approaches the pattern shown by *Mookomys altifluminis*. The anterior loph of M_1 is the widest part of the whole series, though all four lophs of M_{1-2} are of essentially the same width. The general character of M_{1-2} is the same as in *Perognathus*, each being composed of six cusps, three per loph. The union of the cusps to form lophs is rapid, as may be seen in the holotype (fig. 39), which is still sufficiently adolescent so that the

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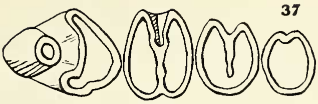

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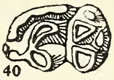

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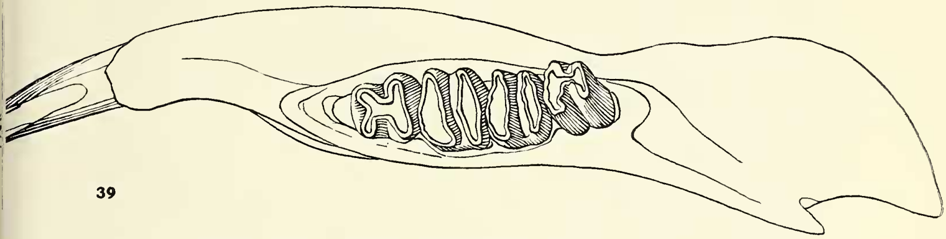

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FIG. 36. *C. nebraskensis*, C. M. no. 10193, LP^4, × 10.
FIG. 37. *C. nebraskensis*, C. M. no. 10170, LP^4—M^3, × 10.
FIG. 38. *C. nebraskensis*, C. M. no. 10193, LM^3, × 10.
FIG. 39. *C. nebraskensis*, C. M. no. 10193, lower jaw with LP$_4$—M$_3$, ×10.
FIG. 40. *C. nebraskensis*, C. M. no. 10168, PdR$_4$, × 10.

epiphyses are not fused to the shafts of the long bones. The traces of the cusps are not retained as irregularities in the outline of the lophs for as long as in *Perognathus*, a definite advance toward *Dipodomys*. In some specimens of *C. nebraskensis*, the lophs first unite at the buccal side of the crown of the lower molars, forming a U. In others, the first point is between the buccal margins of the metaconid and entoconid, resulting in what is here called the H-pattern, especially characteristic of the Dipodomyinae, though occurring in the other subfamilies. Whichever type of union is the first to occur, the other follows almost immediately after, with very little time interval. M$_{1-2}$ are subequal in size.

M$_3$ resembles M^3 in that, while the anterior crest is tricuspidate, the posterior one contains but two cusps, the hypostylid apparently being absent. The two lophs unite at about the middle of the hypolophid, or one third of the distance from the lingual margin of the metalophid (fig. 39), forming a very clear H. M$_3$ is slightly smaller than the lower premolar.

One specimen, C. M. No. 10168, a right lower jaw, contains the deciduous premolar, together with the first molar (fig. 40). The pattern of the deciduous premolar, while distinct from that of *Microdipodops* or *Dipodomys* (figs. 33 and 68) is, nevertheless, much closer to them than it is to the corresponding tooth of *Perognathus hispidus* *paradoxus* (fig. 26), the most advanced type found among the species of *Perognathus* studied. The tooth of *Cupidinimus* helps to indicate the manner in which the *Dipodomys* type of dP_4 was derived from one similar to that of *Perognathus*, although in some respects it is more specialized than any other deciduous premolar studied. The tooth of *Cupidinimus* consists of four primary cusps, as in the other genera. As in *Dipodomys m. merriami*, the cusps of the anterior loph are close to each other and to the anteroconid, which is between the protoconid and mesoconid, instead of being anterior to the mesoconid as in *Microdipodops* (fig. 33). The cingulum extends from the valley between the protoconid and mesoconid, along the anterior, external, and posterior sides of the tooth, as in *Microdipodops*, developing a prominent cusp between the hypoconid and metaconid, as well as a mesostylid, a hypostylid, and three poorly differentiated antero-external stylids (fig. 40). In *Dipodomys*, the cusps which have been derived from the cingulum of *Cupidinimus* are somewhat elevated, and considerably broadened, as well as more separated from each other, so that the suggestion of cingular origin in that form is partly obliterated. In *Perognathus* and *Cupidinimus*, the connection between the anteroconid and the two cusps of the protolophid is between the center of the anterior cusp and the space between the two posterior cusps, or between the anterior cusp and each of the others. In *Dipodomys*, the union varies from being the same as in these other two genera, to being between the mesoconid and the buccal margin of the anterior cingulum. *Cupidinimus*, then, while generally similar to *Microdipodops* and the Heteromyinae in the structure of this tooth, which in all of them seems to be a quadritubercular tooth with additional cusps derived from a buccal, anterior, and occasionally posterior, cingulum, is much closer, fundamentally, to that in *Dipodomys*, and effectually bridges the structural gap between *D. m. merriami* and *P. hispidus paradoxus*, in that it shows without any doubt that the accessory cusps of the former are merely buds from an expanded cingulum.

A casual inspection of the skull (fig. 41) seems to show more resemblances to *Perognathus* than to *Dipodomys*. Closer study, however, reveals many significant similarities to the latter genus, which will be brought out below. The skull does not appear, for instance, to have a mastoid region any more inflated than that of *Perognathus*, but this is partly due to the crushing and destruction of that part of

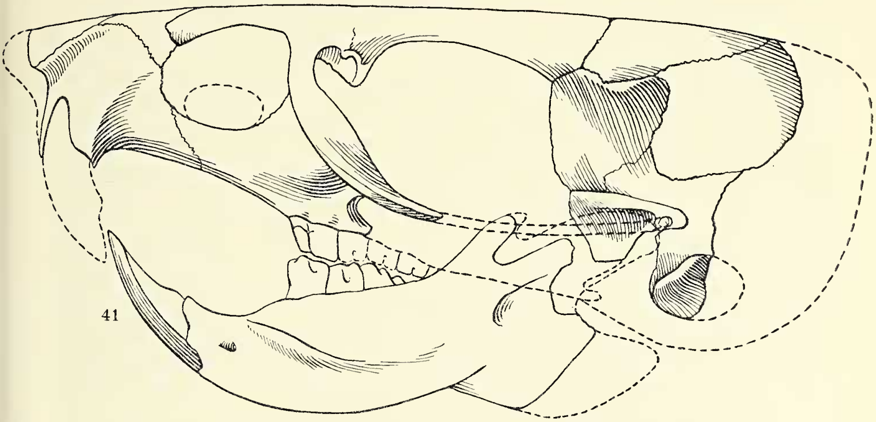

FIG. 41. *C. nebraskensis*, C. M. no. 10193, skull and lower jaw, × 5.

the skull, and only partly to the fact that it is less inflated than in *Dipodomys*. The skull is crushed in nearly as many different directions as possible. The frontals are arched above the rest of the skull from this cause, and the posterior half is twisted about the longitudinal axis of the skull with respect to the anterior half. The effects of crushing have been eliminated to as great an extent as possible in the drawing of the skull, largely by comparisons with the skull of *Perognathus*.

The nasals as preserved are shorter and less inflated than in *Perognathus*, but part of this is due to their tips having been broken off. They do not, however, show the pronounced tubular conditions found in *Dipodomys*. The infraorbital foramen seems as far forward as in the latter genus, although, as its edges are much broken, there may be some error as to its exact position and boundaries. It is entirely possible that the foramen is further forward than in *Perognathus*, and as far forward as in *Dipodomys*. The entire zygomasseteric structure of *Cupidinimus* is close to that in these two heteromyids, and shows no signs of approach toward the conditions found in *Paramys*. This is not surprising, the only Cricitine that Schaub found showing any approach to the *Paramys* type being *Cricetops* of the Oligocene (Schaub, 1925; Matthew and Granger, 1923). It is possible that, when specimens shall be found showing this region in *Heliscomys* or other Oligocene heteromyids, an intermediate type of zygomasseteric structure may be discovered, but it is equally likely that, by the time the Oligocene members of the family had been reached, the chewing habits of the later heteromyids had already been acquired, and hence the typical heteromyid zygomasseteric structure was present. Other families of rodents show a similar rapid development of the progressive structure in this region at a very early date. In the late Oligocene and early Miocene Geomyidae, the zygomasseteric structure was practically identical with that of the modern members of the family. The maxillary has been carried forward on the face by the expansion of the masseter, forcing the infraorbital foramen before it. The zygomatic process of the maxillary of *Cupidinimus* is definitely wider antero-posteriorly than is that of *Perognathus*, and shows the initial step in the process which would lead to the great enlargement of the process in *Dipodomys*. The posterior end of the process, articulating with the jugal, is heavier than in *Perognathus*.

The lacrymal is similar to that of *Perognathus*, being a small bone articulating with the frontal and maxillary at the anterior end of the orbit, but not helping to roof the anterior part of the orbit, as in *Dipodomys*, where it comes into close contact with the expanding zygomatic process of the maxillary. The dorsal surface of the frontal is similar in all the genera, except that in *Perognathus* it extends as far caudad as the anterior end of the glenoid, whereas in *Dipodomys* and *Cupidinimus* it does not. The lateral margin of the frontal slightly overhangs the orbit in this last, anticipating the much greater overhang in the kangaroo rat.

The parietals have a larger lateral extent in *Cupidinimus* than in either of the recent genera, as they are not entirely removed from the temporal foossa as in both *Perognathus* and *Dipodomys*. There is no trace of the notch for the temporalis which has been developed in *Microdipodops*, the muscle apparently being much the same as in *Dipodomys*, but the arrangement of the bones was slightly different. This means that the dorsal expansion of the alisphenoid and squamosal was smaller in the fossil form. There is no trace of a process of the parietal between the squamosal and the mastoid, a resemblance to *Dipodomys*, where it is either entirely absent, or extremely minute. The shape of the parietal is intermediate between that of the more primitive species of *Perognathus* and that of *Dipodomys*, the former being square and the latter almost triangular. The change of shape is brought about by the advance of the mastoid, cutting off the postero-lateral corner of the bone, which was originally square or pentagonal, as in *Heteromys*. The parietal of *Cupidinimus* is about the shape of the state of Nevada, as in the members of the subgenus *Perognathus*. In the subgenus *Chaetodipus*, the mastoid is limited almost exclusively to the lateral surface of the skull, and does not crowd the parietal and interparietal to any great extent. In *Perognathus* (*Perognathus*), the mastoid has advanced onto the dorsum of the skull, paralleling the situation found in *Cupidinimus*. In *Dipodomys*, the interparietal and the branches of the supraoccipital embracing it are compressed by the mastoids until these latter almost, or even actually, meet on the dorsum of the skull. The advance of the mastoids forces the parietals back *pari passu*. In *Cupidinimus*, the parietals have retreated about half the distance that they have gone in *Dipodomys*. The interparietal is about 4.7 mm. wide. In *Perognathus fallax fallax* it is about 7 mm. wide. In the various species of *Dipodomys*, it ranges from 3 mm. down to no visible exposure, although the skull is considerably larger than in *Cupidinimus* and *Perognathus*. The exoccipital embraces the postero-lateral margins of the interparietal as in other heteromyids, but does not surround it as fully as in *Dipodomys* and *Microdipodops*, due to the lesser expansion of the mastoid region. The occipital forms considerably more of the dorsum of the skull than it does in *Perognathus*. It extends as far forward in *Dipodomys*, but does not have as great a width, having been compressed by the bullae.

The mastoid is filled with cancellous bone as in the living Perognathinae and Dipodomyinae. The open spaces are smaller than in the ricochetal genera, closely approaching those species of *Perognathus* with bullae about the same proportionate size. The squamosal reaches the frontal as in *Perognathus*, not yet having been separated from it as in *Dipodomys*, where the alisphenoid intervenes. The latter has been lost from the skull of *Cupidinimus*, and its relations cannot be determined. The glenoid is more nearly like that of *Perognathus*, with the zygomatic process of the squamosal not firmly united to the bulla as in *Dipodomys*, but still coming into contact with it, which is not the case in *Perognathus*. The auditory meatus is definitely lower than in *Perognathus*, and much lower than in *Dipodomys*. It opens caudad as in *Dipodomys* rather than dorsad as in *Perognathus*. This is due to the inflation of the anterior lip of the meatus, although the amount of inflation is much less than in *Dipodomys*. Similar inflation occurs in the subgenus *Perognathus*. The bullous portions of the tympanic and mastoid may connect, in *Cupidinimus*, through the anterior lip of the meatus, as in *Dipodomys*, as well as directly, posterior to the meatus, as in both *Dipodomys* and *Perognathus*, though this cannot definitely be determined without better material. The zygomatic process of the squamosal comes into contact with the tympanic above the meatus, rather than being approximated to its anterior margin, as in *Perognathus*.

On the whole, the skull, while superficially resembling *Perognathus*, shows, on further study, numerous fundamental resemblances to *Dipodomys*. In almost every respect in which *Dipodomys* differs from *Perognathus*, *Cupidinimus* resembles the former, though the character is less pronounced in every instance. The auditory region seems to have been more inflated than in most species of *Perognathus*, and may have been as much so as in *Dipodomys compactus*. The skull characters add to the evidence derived from the teeth, that *Cupidinimus* belongs to the Dipodomyinae, and very probably represents the ancestral form from which *Dipodomys* was derived. The resemblances of the skull to that of *Microdipodops* are greater than those to *Perognathus* in many respects, but most of these are parallelisms, and there are many more points of approach to conditions in *Dipodomys*.

The jaw is slender, as usual among heteromyids (figs. 39, 41, 42). The mental foramen is far forward, being about two thirds of the distance from P_4 to the alveolus of the incisor. The masseteric ridge strikes the diastema at about the middle, the anterior end of the crest curving dorsad at a moderate angle. In some specimens, there is a slight indication of the refolding of the crest described below as a common characteristic of *Dipodomys*. This is, however, never strongly developed, and is entirely absent in many specimens. There is a foramen on the condyloid process in about the same position as that in *Perognathus*, but no trace of grooving or pitting between M_3 and the base of the coronoid, and no foramen in that position, was found in any specimen of *Cupidinimus*. The foramen in the condyloid process

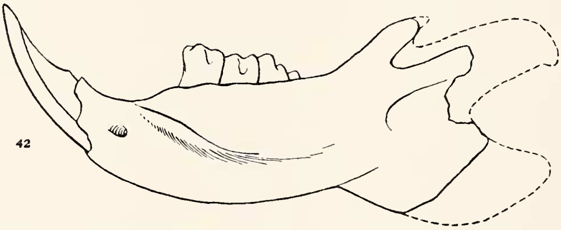
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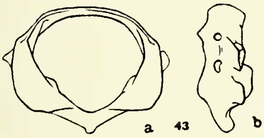
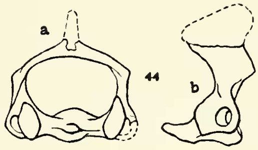
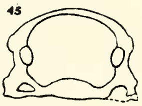
Fig. 42. *C. nebraskensis*, C. M. no. 10193, Lower Jaw, × 5.

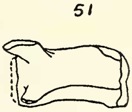
is further forward than in *Heteromys* and *Liomys*, but not as far as in *Microdipodops*. The position of the foramen, as well as of the mental foramen and masseteric crest, vary in different individuals, being closer to the conditions in *Dipodomys* in some specimens than in others. The angle seems to be about as large as in *Perognathus*, and about equally everted. As in all heteromyids, the coronoid process is weak, and slopes backwards, correlated with a weak temporal muscle. The grinding surface of the lower cheek teeth slopes downwards toward the rear.

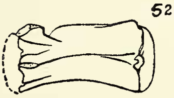
The transverse processes of the atlas are almost entirely in a vertical plane (fig. 43), as in *Dipodomys* and *Perognathus*. The atlantal foramen, on the dorsal side of the bone, is in much the same position

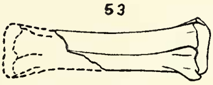












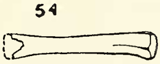


Fig. 43. *C. nebraskensis*, C. M. no. 10193, Atlas, × 5.
(a) anterior side.
(b) left side.
Fig. 44. *C. nebraskensis*, C. M. no. 10193, Axis, × 5.
(a) anterior side.
(b) left side.
Fig. 45. *C. nebraskensis*, C. M. no. 10193, Fourth Cervical, × 5.
anterior side.
Fig. 46. *C. nebraskensis*, C. M. no. 10193, Sixth Cervical, × 5.
left side.
Fig. 47. *C. nebraskensis*, C. M. no. 10193, Second Thoracic, left side, × 5.
Fig. 48. *C. nebraskensis*, C. M. no. 10193, Fourth Thoracic, left side, × 5.
Fig. 49. *C. nebraskensis*, C. M. no. 10193, Second Lumbar, left side, × 5.
Fig. 50. *C. nebraskensis*, C. M. no. 10193, Fifth Lumbar, left side, × 5.
Fig. 51. *C. nebraskensis*, C. M. no. 10193, Second Caudal, left side, × 5.
Fig. 52. *C. nebraskensis*, C. M. no. 10193, Third Caudal, left side, × 5.
Fig. 53. *C. nebraskensis*, C. M. no. 10193, Thirteenth Caudal, left side, × 5.
Fig. 54. *C. nebraskensis*, C. M. no. 10193, Nineteenth Caudal, left side, × 5.

as in these other genera. The inferior median atlantal process is much shorter than in *Dipodomys*, and slightly shorter than in *Heteromys* or *Perognathus*. There is a deep groove above the posterior articular facets, for the second spinal nerve. The posterior half of the arch was certainly without a spine. The spine, if present at all, was definitely smaller than that of *Perognathus* or *Heteromys*, and much smaller than that of *Dipodomys*.

The axis bears a strong, rounded odontoid process (fig. 44). The spine is broken off in the fossil, but must have been of fair size. The vertebro-arterial foramen is confined to the posterior half of the bone. There is no trace of fusion of the axis and third cervical, thus representing a distinctly more primitive stage than does either *Dipodomys* or *Microdipodops*. A well marked median ventral ridge runs the whole length of the centrum, dividing into two small, closely spaced tubercles, just at the posterior edge of the bone. The lamella of the transverse process surrounding the vertebro-arterial foramen is very slender, and the whole process is narrow, antero-posteriorly. This bone differs markedly from that of *Dipodomys* and somewhat from those of *Perognathus* and *Heteromys* in the size of the spine. Even though it is broken off in the fossil, it could not have been large. Its actual size is nearly the same as in the much smaller *P. f. fallax*. Hatt (1932, p. 640) says that the axis and the third cervical are almost always the first vertebrae to fuse in ricochetal forms, *Microdipodops* being the only exception. As the first, second, fourth and sixth cervicals are preserved in *C. nebraskensis*, it is clear that, since they show no trace of such fusion, there could have been none in the centra or transverse processes, and little, if any, in the neural spines. No appreciable spines are present on the post-axial cervicals, a closer approach to *Perognathus* and *Dipodomys* than to *Heteromys*. The small size or entire absence of the spines is partly a function of the small size of the animals. The neck, however, shows definite indications of the shortening found in ricochetors.

The fourth cervical (fig. 45) shows no trace of the knobs on the dorsal surface of the arch described below as existing in *Diprionomys*. There is no median ventral ridge on the sixth cervical (fig. 46). The spines of the dorsal vertebrae (figs. 47-48) are considerably shorter, proportionately, than in *Dipodomys*. Except for a similar shortening of all the processes, the lumbar vertebrae (figs. 49-50) appear very similar in both genera. There appear, however, to be no median ventral foramina in the centra of any of the lumbars that are preserved in the skeleton of *C. nebraskensis*.

The sacrum and pseudosacrum are missing from this skeleton. Among the other material collected from the same locality is a pseudosacrum, composed of three vertebrae, which may belong to this genus, as it is about the correct size.

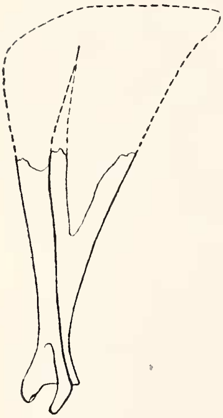
The median ventral foramina of the caudal vertebrae are further forward than in *Heteromys*, and much further forward than in *Dipodomys* (figs. 51-54), being about a quarter of the distance from the anterior end of the bone in the fossil, as opposed to two fifths, and a half, in the two recent genera mentioned. Their presence at all is one of the factors distinguishing this genus from *Microdipodops*. The anterior part of the fourth caudal is much wider than in *Heteromys*, its diapophyses expanding laterally as far as they do in *Perognathus* and *Dipodomys*. The transverse processes point ventrally as well as anteriorly, resembling *Perognathus* and *Dipodomys*, but differing from *Heteromys*.

In general shape, the scapula (fig. 55) is an elongate isosceles triangle, similar in shape to that of *Perognathus* and other quadrupedal heteromyids. As the dorsal half of both scapulae are not preserved, it is impossible to say whether or not the vertebro-axial angle was elongated in the manner so characteristic of *Dipodomys* and *Microdipodops*. Near the distal end of the spine, there is a noticeable curve, though it is not a real metacromion. This is a nearer approach to one, however, than was found in any other heteromyid, the process being very minute in *Dipodomys*, and not seen at all in *Perognathus*. The acromion extends ventrad of the glenoid cavity, as in *Perognathus*, but extends somewhat anterad, instead of continuing the direction of the spine. In *Dipodomys*, the acromion is definitely shorter than in the other two genera. In *Cupidinimus*, as in *Perognathus*, the infra- and supra-spinatus fossae are subequal, whereas in the saltatorial genera, the infraspinatus fossa is greatly enlarged, correlated with the elongation of the postero-dorsal margin of the bone. The cranial border of the scapula of *Cupidinimus* is straighter than that of *Dipodomys*. The lack of expansion of the infraspinous fossa is good evidence that the vertebro-glenoid angle was not greatly produced. A good-sized coracoid process is present.

In *Neotoma*, an entirely non-ricochetal, scampering animal, the supraspinous and infraspinous fossae are about equal in size. In ricochetors, the infraspinous is much larger, the supraspinatus muscle being reduced. Saltators have a falciform gleno-vertebral angle, corresponding with an increase of the teres major. This also gives the serratus magnus better leverage in depressing the posterior part of the scapula and thus aiding in the anterior elevation of the arm. The coracoid seems better developed in *Perognathus* and *Cupidinimus* than in *Dipodomys*, indicating that these forms have stronger short heads of the biceps. The general appearance and more detailed structure of the scapula indicate an animal little, if any, more adapted for riococheting than is *Perognathus*. The resemblances to this last are, in part, at least, a retention of primitive characters. The scapula of *Cupidinimus* probably represents nearly the primitive type for the Dipodomyinae.

The clavicle (fig. 56) is long and slender, resembling that of other heteromyids. No significant variations of this bone were detected within the family.

Detailed comparisons were made between the humerus of *C.*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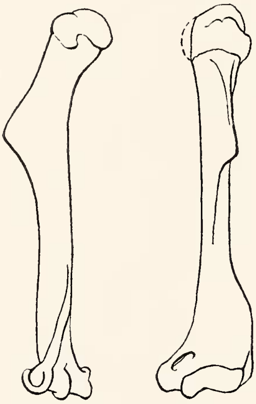
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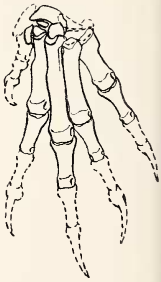
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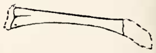
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FIG. 55. *C. nebraskensis*, C. M. no. 10193, Left Scapula, × 5.
FIG. 56. *C. nebraskensis*, C. M. no. 10193, Left Clavicle, × 5. anterior view.
FIG. 57. *C. nebraskensis*, C. M. no. 10193, Left Humerus, × 5.
(a) lateral view.
(b) anterior view.
FIG. 58. *C. nebraskensis*, C. M. no. 10193, Right radius and ulna, × 5. lateral view.
FIG. 59. *C. nebraskensis*, C. M. no. 10193, Left Manus, × 5.

nebraskensis (fig. 57) and those of *Perognathus fallax* and *Dipodomys ordii luteolus*, and more incidental comparisons with other forms. The separation between the head and the greater tuberosity is much better developed in *Cupidinimus* and *Dipodomys* than in *Perognathus*, where there is only a faint groove. *Cupidinimus* and *Dipodomys* appear to be closer to *Paramys* in this respect. The anterior face of the greater tuberosity is poorly defined in *Cupidinimus* as in *Dipodomys* and *Heteromys*. The greater tuberosity is slightly higher than the lesser in *Cupidinimus*, thus distinguishing it from *Dipodomys*, in which the reverse is true. The bicippital groove is well developed and stronger than in *Dipodomys*. The lesser tuberosity is small in all forms. In *Cupidinimus*, the head is subglobular and about the same size as the head of the femur. It is set at an angle of about thirty degrees to the long axis of the shaft, although not separated by any constriction which could correspond to the neck of the femur. The humerus of *Dipodomys* is the same in this respect. In *Perognathus*, the head is not set at so great an angle, although an incipient tendency toward this modification is shown. In all these forms, there has been a considerable rotation of the head from its primitive position, as exemplified by *Heteromys* and *Paramys*, where it is essentially continuous with the main axis of the bone, to a more lateral position. A strong groove is present in *Dipodomys*, on the posterior surface, which is absent in *Perognathus* and *Cupidinimus*.

The deltoid process is large and extends throughout the proximal third of the bone. It ends distally in a strong deltoid process, which is simple in *Cupidinimus* as in *Perognathus* and *Paramys*, with no trace of the strong knob which occurs on the lateral margin of the process in *Dipodomys* and *Microdipodops*. There appears to be a correlation between methods of locomotion and the angle made by the proximal and distal margins of the deltoid process with each other. In *Paramys*, this is about 120°; in *Perognathus*, about 110°; in *Cupidinimus*, about 100°; and in *Dipodomys* and *Microdipodops*, little, if any, greater than 90°. In *Paramys* and *Heteromys*, the distal end of the deltoid process is about 35% of the length of the bone from the distal end. In the other genera, it is approximately 60%. In *Cupidinimus*, *Perognathus* and *Dipodomys*, the deltoid crest ends sharply, almost forming a right angle with the shaft of the bone; in *Microdipodops*, it actually forms a right angle; whereas in *Heteromys*, the process slopes subequally in both directions from its highest point.

This is a point of close similarity with *Paramys*, from which the deltoid process of *Heteromys* differs chiefly in being somewhat higher and definitely more proximad.

The distal half of the bone carries a strong supinator crest and an entepicondylar foramen, which last is present in all of the Heteromyidae. The supinator crest seems better developed in *Cupidinimus* than it is in *Dipodomys*, and hence is much longer than in *Microdipodops*. The angle at its proximal end is about the same in *Cupidinimus*, *Perognathus* and *Microdipodops*, and steeper in all than in *Dipodomys*. In this last, the trochlea extends slightly further distad to the supratrochlea than it does in *Cupidinimus* or *Perognathus*. In *Perognathus*, in fact, the distal end of the bone is almost a straight line, at right angles to the axis of the shaft.

The humerus, as a whole, seems more like that of *Dipodomys* than that of *Perognathus*, both in general proportions and in the relations and shapes of the processes. In some respects, it is more primitive than the humerus of the latter genus, and in some respects more advanced. It is smaller in proportion to the femur than in *Perognathus*, but larger than in *Dipodomys* (see Table V), representing an intermediate stage in the transformation of a scampering into a ricochetal form. The fact that the proximal end is more massive than the distal is a resemblance to *Perognathus*, and is probably a primitive condition retained independently by the two forms.

The radius and ulna (fig. 58) are very similar to the corresponding bones of both *Perognathus* and *Dipodomys*. There seems to have been very little variation in the characters of these two bones within the family. They are distinctly arched apart in their proximal half, but no more so in *Cupidinimus* than in the living genera of heteromyids. The two bones, although closely appressed distally, are separate in all forms observed. The olecranon is definitely shorter in *Dipodomys* than in the other genera. In *Cupidinimus*, *Heteromys* and *Perognathus*, the humerus and radius are essentially of equal length. In *Paramys*, the humerus is the longer. In *Dipodomys*, the radius is 20% longer than the humerus. This shortening of the upper arm is merely one aspect of the shortening which is proceeding throughout the entire fore limb in the progressive ricochetal adaptations (see Table V).

The manus (fig. 59. See also fig. 152) has about the same general proportions as does that of *Perognathus* or *Dipodomys*, and is nowhere near as slender as that of *Microdipodops*. There is no great reduction or specialization of any of the parts other than what is characteristic of the family as a whole. In *Cupidinimus*, the scapholunar, trapezium, trapezoid, magnum and centrale are preserved. The fusion of the scaphoid and lunar, which has taken place in all the members of the Heteromyidae in which the manus is known, represents a distinct advance over *Paramys*, in which form the two bones are still distinct. The scapholunar is not as wide as in *Dipodomys* and *Perognathus*, but otherwise is much the same shape. It sends a process mediad which barely overlaps the trapezium. In *Dipodomys*, this process is much longer, extending over half the length of the trapezium. In *Perognathus* and *Heteromys*, the process is even less well developed than in *Cupidinimus*. In the fossil, as in *Heteromys*, the length of the scapholunar is about the same for ¾ of its width (transverse diameter). In *Dipodomys*, the bone becomes progressively longer from the median almost to the lateral margin. The centrale, in the dorsal aspect, is essentially triangular in *Dipodomys* and *Perognathus*. In *Cupidinimus*, it is more ovate, thus approaching closer to the conditions to be found in *Heteromys* and *Paramys*. In *Cupidinimus*, the trapezium is essentially the same shape—elongate from proximad to distad—as in *Dipodomys*, *Perognathus*, *Heteromys* or *Paramys*. The trapezoid of *Cupidinimus*, while separating the trapezium from the centrale, does not keep them far apart, whereas in *Dipodomys*, it extends in a large process between them, and has a broad facet articulating with the scapholunar. There is no trace of this articulation either in *Cupidinimus* or in *Paramys*. In *Heteromys* and *Perognathus*, the trapezoid is even smaller, allowing the median portion of the large centrale to articulate with the trapezium. In *Dipodomys* and *Heteromys*, the articulation between the trapezoid and metacarpal II continues as an almost straight line into the articular surface between the centrale and the magnum and that between the scapholunar and the unciform. This condition is approached in *Cupidinimus*, which has progressed far from the brick-like carpus of *Paramys*. Of all the modern genera, *Perognathus* is the closest in this portion of the manus to *Paramys*. In *Dipodomys*, the magnum sends only a small proximal process into articulation with the scapholunar, whereas in *Cupidinimus*, this process is quite broad, being almost half the width of the magnum. In *Paramys*, the magnum and intermedium are in contact for almost their entire widths. *Heteromys* and *Perognathus* are definitely the most specialized heteromyids seen in this respect, the unciform reaching the centrale, and sending a broad process between the magnum and the scapholunar. A similar process is present in *Dipodomys*, though it is somewhat narrower. Apparently, no such process was present in *Cupidinimus*. In *Paramys*, while the articulation of the unciform and lunar is broad, it does not separate the magnum from the latter.

In *Dipodomys* and *Cupidinimus*, metacarpal III is about three times as long as the carpus; in *Heteromys*, *Perognathus* and *Paramys*, it is about three and a half times its length. The metacarpals and phalanges are definitely shorter in *Cupidinimus* than in *Perognathus* by about ten or fifteen percent for a given body size. The difference is the other way with *Dipodomys*, where the metacarpals and phalanges are proportionately still shorter than are those of *Cupidinimus* (see Table III). In *Microdipodops*, the tendency appears to have been in the other direction, tending toward a more elongate manus.

The pollex seems more reduced than in *Perognathus*, although, as it is absent in the fossil, it is difficult to do more than estimate its length. All the heteromyids, however, have a much less reduced pollex than is found in any described species of *Paramys* with which I am familiar, which would indicate that none of these species of *Paramys* would be likely to be ancestral to the heteromyids, unless there had been a reversal of evolution. As, however, on other grounds the Bridger species of *Paramys* would not be considered as possible ancestors of the heteromyids, and as the manus is not known in the Lower Eocene species, this specialization does not seem especially significant.

It is worthy of note in how many points of detail the manus of *Cupidinimus* resembles that of *Dipodomys*. In most of the characters which differ markedly from those of *Dipodomys*, there is a striking resemblance to the conditions found in the Middle Eocene forms of *Paramys*. The manus seems to be that of an incipient *Dipodomys*, which is identical with the conclusions reached from other parts of the skeleton. The manus also provides another feature helping to differentiate this subfamily from *Microdipodops*, in spite of the numerous structural parallels.

The ilium and dorsal part of the ischium are represented from both sides of the fossil, and are essentially complete (fig. 60). The ilium is quite close to that of *Perognathus*. It differs from the one in *Dipodomys* in that the ventral, iliac fossa is much smaller than the

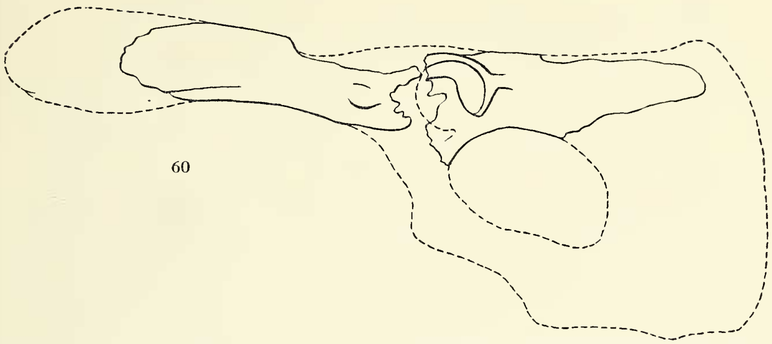


FIG. 60. *C. nebraskensis*, C. M. no. 10193, Left pelvis, Lateral view, Restored from *Perognathus*, × 5.

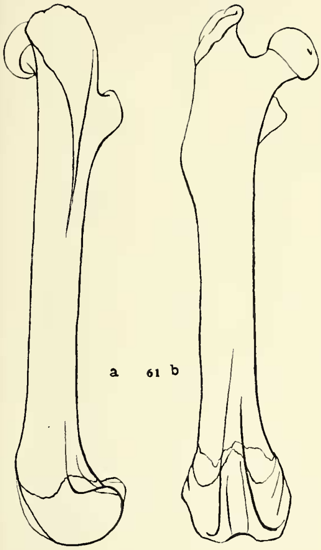
dorsal, gluteal one, as in *Perognathus*, although the demarcation between the fossae is indistinct, as the tip of the ilium is broken off. A strong tubercle for the rectus femoris is present, anterior to the acetabulum. From the radius of curvature of the portion of the ilium that is present, it can be seen that the proximal end was not everted as much as in *Perognathus*, being close to *Dipodomys* or *Heteromys* in this respect. The notch on the dorsal margin of the ilium is similar in position to that in *Perognathus;* the similar notch of the ischium is less marked than in *Perognathus*, thus being closer to *Dipodomys*. This latter notch is definitely more anterior than that in *Perognathus*. No crest is visible on the dorsal part of the ischium, thus differing from *Dipodomys* and approaching *Perognathus* and *Heteromys*. Howell (1932, p. 521) says that this crest is doubtless correlated with increased efficiency, and stronger and more tendinous origins, of the hamstring muscles in *Dipodomys*, which are of major importance in saltation. To this extent, it would indicate less saltatorial ability on the part of *Cupidinimus*. While the exact shape of the obtuator foramen can not be determined, due to the lack of preservation of the pubis, it appears to have had the same shape as that of *Perognathus*. It was certainly not as much compressed dorso-ventrally as that of *Microdipodops*, and probably not as much so as that of *Dipodomys*, nor does it appear to have been subtriangular. There is no trace of any rugosity near its anterior margin to which the ligament occurring in *Dipodomys* and *Microdipodops* could have been attached.

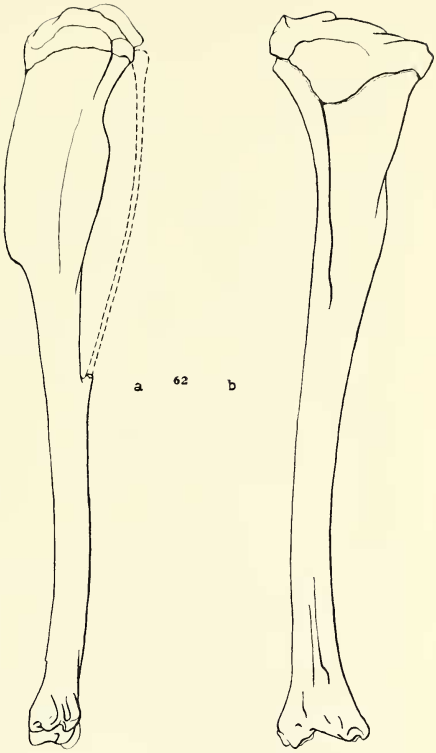
The shaft of the femur is quite straight, in this more closely resembling *Dipodomys* than *Perognathus*, and *Heteromys* than either (fig. 61). In *Dipodomys*, the high point of the third trochanter is 7.3 mm., or 25.5% of the length of the bone, from the proximal end; in *Perognathus*, 6.0 or 27.5%; in *Cupidinimus*, 3.75 or 25.3%; in *Liomys*, 6.6 or 31.2%; in *Heteromys*, 8.7 or 34.2%; and in *Paramys delicatus*, 30.0 or 30.6%. In this respect, *Cupidinimus* is more like *Dipodomys* than like *Perognathus*. If *Paramys* represents the primitive situation, the process has moved distad in *Liomys* and *Heteromys*, and proximad in the other forms. The third trochanter is smaller in actual size in *Cupidinimus* than in either *Perognathus* or *Dipodomys*, indicating that *Cupidinimus* had smaller gluteus superficialis and adductor brevis muscles than do the other two. In *Dipodomys*, the gluteus superficialis is one of the principal flexors of the thigh and the adductor brevis one of the powerful extensors thereof, thus apparently indicating less jumping ability in *Cupidinimus* than in *Dipodomys*.

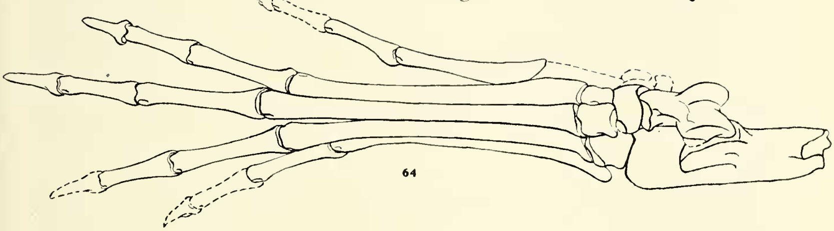
The neck of the femur is more nearly the same diameter as the head in *Cupidinimus* than in *Dipodomys*. The lesser trochanter is smaller than in *Perognathus fallax*. The great trochanter is higher in *Cupidinimus* than in *Perognathus* or *Dipodomys*. The figures are: in *Dipodomys*, 0.85 mm. higher than the head, or 3% of the length of the femur; in *Cupidinimus*, 0.60 or 4%; in *Perognathus hispidus paradoxus*, 0.50 or 2.3%; in *P. flavescens*, 0.15 or 1.5%. If the height of the great trochanter above the head is a measure of saltatorial adaptation among heteromyids, as Mr. H. C. Raven informs me it is among kangaroos, *Cupidinimus* would be even more saltatorial than *Dipodomys*. In *Heteromys longicauda*, the great trochanter extends 0.95 mm. above the head, or 3.7%, more than in *Perognathus* or *Dipodomys*, but less than in *Cupidinimus*. This, together with the fact that the great trochanter definitely extends beyond the head in *Castor*, would seem to indicate that, among rodents, there is no connection between the amount of extension of the great trochanter beyond the head and leaping ability.

The angle between the shaft of the femur and the head is 48° in *Cupidinimus*, 50-60° in *Perognathus*, 60° in *Dipodomys*, and 65° in *Heteromys*, a series of measurements whose significance is uncertain.

As in all heteromyids, the tibiofibula is the largest bone in the body (fig. 62). In *Cupidinimus*, as in *Dipodomys*, the two are fused for slightly more than half their length. In *Perognathus*, the percentage of fusion is slightly less than 50, while in *Microdipodops* the percentage







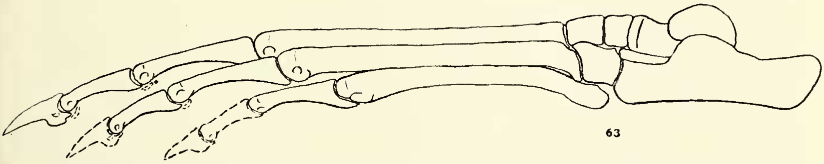


FIG. 61. *C. nebraskensis*, C. M. no. 10193, Left Femur, × 5.
Distal end restored from opposite side.
(a) lateral view.
(b) anterior view.
FIG. 62. *C. nebraskensis*, C. M. no. 10193, Left Tibiofibula, × 5.
(a) lateral view.
(b) anterior view.
FIG. 63. *C. nebraskensis*, C. M. no. 10193, Left pes, lateral view, × 5.
Calcaneum restored from another specimen.
FIG. 64. *C. nebraskensis*, C. M. no. 10193, Left pes, × 5.

is definitely more (see Table III). The tibia is distinctly longer than the femur, indicating (Howell, 1932, p. 524) saltatorial specialization. In *Perognathus*, six specimens representing six different species and subspecies were measured, giving an average length of tibia as 114.4% of the femur, the maximum being 126.1 and the minimum 100.0. In *Dipodomys*, also with six specimens measured, the corresponding figures were 132.6, 141.2 and 113.9. The figure for *Cupidinimus*, 129.6, is nearer the average for *Dipodomys* than that for *Perognathus*, but is almost within the range of variation of the latter. It serves to indicate a definite tendency toward saltatorial specialization in *Cupidinimus*. The cnemial crest is lower in *Cupidinimus* than in *Dipodomys* or *Perognathus*. As in *Diprionomys*, the medial malleolus is the longer. There is no evidence of any tendency in the fossil for an approach to the type of tibia and fibula found in *Paramys*, where the two bones are entirely separate, but lie close together in the distal third of their length. *Cupidinimus*, as has been pointed out, is already more specialized in the amount of fusion than are the living members of *Perognathus*.

In the main outlines and general appearance, the pes (figs. 63-64) is distinctly closer to that of *Dipodomys* than it is to that of *Perognathus*. The transverse compression of the metatarsals at their centers so that the diameter of the pes is here less than at their proximal ends, and the marked flare of the distal ends of the toes, are quite similar to the situation in *Dipodomys*, although developed to a slightly lesser extent, and probably served to increase the stability of the animal in the ricochet.

The astragalus is more elongate than that of *Paramys* (Matthew, 1910, fig. 5) and about as much so as that of *Perognathus* or of *Dipodomys*. The tibial keel is considerably shorter than the fibular, as in *Diprionomys agrarius*, *Microdipodops* and *Dipodomys*. In *Perognathus*, the anterior end of the calcaneum is elongate to about the same degree as is that of the astragalus, the two ending at nearly the same level, so that there is a very slight cubo-astragalar contact, although the lateral margin of the calcaneum extends definitely further distad (see fig. 153). This same contact likewise occurs in some species of *Paramys*, although the astragalus and calcaneum are so close to being of the same length that apparently sometimes this contact and sometimes the alternative naviculo-calcaneal contact occurs. In *Cupidinimus*, however, there is a clearly developed contact between the calcaneum and the navicular, the medial margin of the calcaneum being the most distal part of the bone. In *Dipodomys*, the anterior end of the calcaneum has moved forward until it is on a level with the anterior end of the navicular. In the specimen of *D. merriami* studied, there was no calcaneal-cuneiform contact. In *D. ordii luteolus*, A. M. N. H., D. C. A. No. 184, the two bones apparently just come into contact with each other. In *D. o. luteolus* A. E. W. No. 1302, they do not quite meet. But apparently there is a tendency for this contact to develop in more progressive forms of *Dipodomys* (see below, p. 152). The navicular of *Cupidinimus* resembles that of *Dipodomys* in the long ventral process, extending anteriorly beneath the cuneiforms, which is, however, shorter than in *Diprionomys*. The process is shorter, relatively, than that of *Dipodomys*, being, in *Cupidinimus*, only about twice the length of the dorsal surface of the bone, while in *Dipodomys*, it is about two and a half times that length. The length of the navicular is essentially uniform in *Cupidinimus*, although it shortens slightly, toward the median side. The cuboid is similar in the two forms, with a ventral process approximated to that of the navicular. To these ventral processes are attached the tendons of the plantaris (Howell, 1932, fig. 20, p. 473). The cuboid of *Cupidinimus* is more compressed antero-posteriorly than in either *Perognathus* or *Heteromys*, but much less so than in *Dipodomys*, correlated with the calcaneal-navicular contact. In all these forms, there is a dorsal process, on the median side of the cuboid, curving proximad, between the calcaneum and the cuneiform, although it is greatly reduced in *Cupidinimus* and *Dipodomys*. The ectocuneiform has a slight hour-glass shape in its dorsal aspect, definitely suggestive of *Dipodomys* and *Perognathus*. The mesocuneiform is much larger than in either *Heteromys*, *Perognathus* or *Dipodomys*, being only slightly smaller than the ectocuneiform, instead of having only about half to a third of its surface area. In this last respect, *Cupidinimus* seems very close to *Paramys*, and appears the most primitive of the heteromyids. The change in size of the mesocuneiform is correlated with the proximal movement of the end of metatarsal II.

The foot is arched in cross section much as in *Dipodomys*, and more so than in *Perognathus*. The distal ends of the metatarsals do not spread as much as in *Dipodomys*, but definitely more than in *Perognathus*. The lateral digits are longer proportionately than in either *Perognathus* or *Dipodomys*, but the central three seem to make a more unified group than in *Perognathus*, and appear quite suggestive of *Dipodomys* or *Microdipodops*.

Heteromys, *Dipodomys*, *Microdipodops* and *Perognathus* have all elongated the metatarsals as compared to the tarsus, when contrasted with *Paramys*, to a similar extent, *Microdipodops* having the greatest elongation. *Perognathus* and *Microdipodops* have elongated the phalanges the most, and *Heteromys* the least. Or, in other words, the tarsus of the Perognathinae has increased the least in length. *Cupidinimus* seems most like *Perognathus* in these characters. The tarsus has increased least in proportion of all three sections of the foot, less even than in *Perognathus*. In *Paramys*, the foot is three times as long as metatarsal III. In all the other forms, it is in the neighborhood of 2.5 times as long, the figure being larger in *Cupidinimus* and *Heteromys* than in the other forms. In *Cupidinimus*, metatarsals II-V are nearly the same length, the third being about $\frac{2}{5}$ (.42) the length of the tibia. In *Perognathus*, III is .42 the length of the tibia, and in *Dipodomys* .43, essentially as in *Cupidinimus*. In *Microdipodops*, III is .45 the length of the tibia. In *Heteromys*, I and V are definitely shortened, the others being subequal in length. Here III is .46 the length of the tibia. In *Paramys*, the figure is .29. In all the heteromyids, the hallux is about the same proportionate size as in *Paramys*. In *Cupidinimus* and *Perognathus*, the fifth metatarsal is about 12% shorter than the third. In *Paramys* (Matthew, 1910, fig. 5), V is about 22% shorter than III. This is another character in which *Cupidinimus* seems more primitive than any species of *Paramys* in which the pes is known, and closer to *Dipodomys* than to any other heteromyid. In this last genus, there is a 9 to 10% difference in length between III and V. The hallux is greatly reduced or even absent in *Dipodomys*, a reduction of which there is no apparent foreshadowing in *Cupidinimus*. As, however, some species have lost the hallux and others have not, it would seem that *Dipodomys* is at present in a condition of definite evolution as regards this character, and apparently fairly rapid evolution, since there has not been an opportunity to make great changes in other characters to help differentiate the five-toed from the four-toed animals. In *Perognathus*, the hallux also shows considerable reduction. The ungual phalanges of *Cupidinimus* are about two fifths as long as are the median, and a third as long as the proximal phalanges. In *Dipodomys*, they are about as long as the medials and about half as long as the proximals. In *Perognathus*, the unguals are almost as long as the medials, and in *Heteromys* about three fifths as long. *Paramys* is about as *Heteromys*, so the ungual phalanges of *Cupidinimus* would seem to have suffered reduction.

Leaving the pes out of consideration, both *Heteromys* and *Perognathus* have elongated their hind limbs to about the same degree when compared with *Paramys*—6%. In *Cupidinimus*, the figure is 18%; in *Dipodomys*, 33⅓%. Including the pes, however, *Heteromys* has elongated the hind leg 9%; *Perognathus* 14%; *Cupidinimus* 18%; and *Dipodomys* 36% as compared with *Paramys*. From the point of view of these ratios, as well as in numerous other respects, *Heteromys* is the nearest of the heteromyids to *Paramys*, and thus, presumably, the most primitive. In both ratios, *Cupidinimus* is intermediate between *Perognathus* and *Dipodomys*, but nearer the former. In *Cupidinimus*, the revised intermembral index is 43, as compared with 35 for *Dipodomys*, 43 for *Microdipodops*, 48 for *Perognathus*, 42 for *Diprionomys*, 50 for *Heteromys*, 60 for *Neotoma*, and 53.3 for *Paramys*. As *Cupidinimus* and *Diprionomys* have essentially the same indices as does *Microdipodops*, it would appear that they are equally able ricochetors. There is a strong correlation among rodents between a highly inflated auditory region and ricochetal locomotion, though the reason for this correlation is obscure. The inflated auditory region of *Cupidinimus* is of considerable significance when taken together with the limb ratios outlined above.

Dr. R. T. Hatt suggested (verbal communication) that the lack of fusion of the cervical vertebrae of *Cupidinimus* (and of *Diprionomys;* see below, p. 185) might indicate that the animal was not a ricochetor, and might possibly tend to out-weigh the evidence of limb proportions. It seems logical to suppose, however, that the fusion of the cervical vertebrae would be an adaptation to an established ricochetal gait, and not a prerequisite for its development. That is, the fusion of the cervicals would follow the acquisition of the new method of locomotion, by a longer or shorter period, and would increase the adaptation of the animal to its new habits, whereas the lengthening of the hind limbs would of necessity immediately precede the acquisition of the ricochetal locomotion. Whether the time interval between the development of ricocheting and the fusion of the cervicals would be long or short would depend merely on the length of time before the necessary mutation or mutations appeared.

Leaving aside the question of the fusion of the cervical vertebrae, which seems to be a lately acquired character progressively developed in *Dipodomys*, and one especially adapted to its present facies, the resemblances between *Cupidinimus* and *Dipodomys* are extremely striking, amounting to a demonstration of relationship, and suggesting that the former is at the very least the structural ancestor of the living genus. The similarities with *Perognathus* are largely resemblances due to partial retention of primitive rodent characters, of primitive heteromyid characters, to parallel evolution in similar stages, or else turn out, on closer study, not to be real resemblances at all.

The restoration of *Cupidinimus nebraskensis* (fig. 35) has been made from a careful comparison of the skeletons and postures of *Perognathus* and *Dipodomys*, as well as from observations on a living *Dipodomys*, and probably represents something fairly close to its actual appearance and position in life. As cheek pouches are universal in the living members of the family, as well as in the related geomyids, it is probable that they were present in this genus too. No attempt has been made at a detailed restoration of the soft anatomy, merely an outline being supplied to show its general character.

The Valentine matrix is a fine grained arkosic sand, a large part of the grains running from 0.2 to 0.7 mm. in diameter, with the smaller ones forming by far the largest quantity of the matrix. The grains are predominantly clear, crystalline, white quartz, well rounded, but without any visible pitting. A considerable portion of the total bulk —perhaps 20%—is a very fine sand, below 0.1 mm. in diameter. A small portion of the larger grains are of other than the white quartz—perhaps 5%. Of these, the largest part seem to be darker colored quartz, the feldspars being largely fine grains. Mr. Howard informs me that there is no evidence of volcanic material in the sample submitted to him.

The larger part of the fauna associated with *C. nebraskensis* are forms which would occur in a plains facies. The modern *Dipodomys* does not require a desert environment in the sense in which the word desert is frequently misunderstood—entire absence of vegetation, or of any vegetation but cactus. It lives in all of the arid portions of western United States, occurring in the same type of habitat as the modern prong-horns, the imported horses, cattle and sheep, the coyote, the prairie-dog, and numerous other small rodents. Many of these forms have relatives in the Valentine fauna. There is a general absence of thick cover of vegetation over such parts of the west as are actually occupied by *Dipodomys*, the main cover usually being sage brush, which is normally rather sparse. It seems logical to believe that the plains at the time of deposition of the Valentine sands were semi-arid, similar in general to the western parts of South Dakota and Nebraska of today, with a few streams rising in the mountains and flowing east across the plains, along which such forms as *Dipoides* and *Teleoceras* may have lived. In an environment such as this, the ricochetal adaptations of *Cupidinimus* would be of considerable assistance in opening a new ecological niche to its possessor—a niche which was developing *pari passu* with the increasing aridity. To the extent that this niche was existing before the evolution of the ricochetors to fit it, and that the evolution of the niche preceded and permitted the evolution of the occupant thereof, the concept of orthogenesis could be applied to this case. But this does not imply any tendency within the animal to orthogenesis, other than continual mutations in all directions, some of which happened to be in the direction of greater ricochetal ability, and would, therefore, have greater survival value.

The sands in which the Valentine fauna is entombed would seem to represent a former channel of the present Niobrara River, which flows only a short distance north of the exposures from which the fossils were recovered, or the channel of a tributary stream. The heteromyids may have been derived from owl pellets left at the foot of a tree near the stream, but such a preponderance of a single species in an owl's food is most unusual. That there must have been other small rodents in the vicinity is shown by the two or three specimens of other forms in the author's collections. The locality where the heteromyids are so abundant may represent a dune or sand flat a short distance from the stream, in which the heteromyids lived and were buried. Other possible hypotheses, such as a sub-aquatic habitat for the animals, appear to be much less likely.

Cupidinimus magnus (Kellogg)

DIPRIONOMYS MAGNUS Kellogg, 1910

Figs. 65-66; Kellogg, 1910, fig. 18; Hall, 1930*b*, figs. 11-12.

Cotypes: U. Cal. Coll. Vert. Pal. No. 12567 and 12568, from the Thousand Creek Pliocene Beds of Humboldt County, Nevada.

Diagnosis: Size large; teeth high crowned but rooted; P_4 wider than M_2; M_2 wider than M_1; P^4 wider than M^{1-3}; anterior part of masseteric ridge steep.

Range: Thousand Creek, Middle Pliocene of Nevada and Benson, Upper Pliocene of Arizona.

One of the most significant features of this species is the great increase in the height of the crown, which is strongly suggestive of affinities with *Dipodomys* or *Microdipodops*, though this species can be ancestral to neither genus, being contemporary with the earliest species of the former, and differently specialized from the latter. The great length of the metalophid of P_4 (fig. 65) differentiates it from *Microdipodops*, and is close to what must have been developing, at about the same time, in the ancestors of *Dipodomys*, probably other species of *Cupidinimus*. The masseteric ridge resembles that of *D. merriami* in its position and direction. From the size of the alveoli, and from Kellogg's measurements, it is clear that the molars are no wider than the premolar, a character found in some forms of *Dipodomys* and in *Microdipodops* (see Table II).

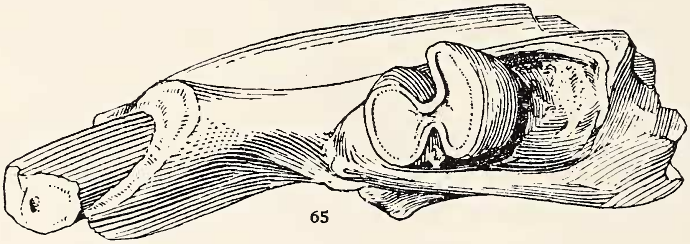


FIG. 65. *Cupidinimus magnus*, After Hall, 1930*b*, LP_4, × 10.

Another specimen, A. M. N. H. No. 21835, collected by J. W. Gidley in March, 1924, from the Upper Pliocene Benson beds near Benson, Arizona, consists of LP^4—M^1, with associated upper incisors, and is tentatively referred to this species (fig. 66). The crowns of the teeth are as high as in the types of *C. magnus*, and the general suggestion of the tooth is of affinities with *Dipodomys*. As roots are present, it can not belong to the living genus. This specimen is approximately the same size as *C. magnus*. It is much worn, but a few interesting observations can be made. The crowns are higher than in any known Tertiary heteromyid other than the two contemporary species of *Dipodomys* and the slightly earlier *C. magnus*. There is almost no differentiation between the two lophs of P^4, which is very suggestive of the kangaroo rats (see figs. 76, 82 and 84). Such a pattern does not appear to develop in any other heteromyids. The progressive decrease in size of the upper molars is carried much further than in *C. nebraskensis*, although it is foreshadowed in that form. Upper incisors associated with the maxilla are grooved as in *Dipodomys*.

While this species is too late in time to have given rise to *Dipodomys*, it is very suggestive of the intermediate stages that must have been represented in the ancestry of that genus, and is an interesting and probably closely related parallel to that line, especially in the additional character of having developed grooved upper incisors, if the ones with the fossil are correctly associated. They are of the right size and general appearance to belong to a heteromyid of this size. Hall (1930*b*, p. 303) suggested that this species had affinities with *Dipodomys*, although he considered it even closer to *Liomys*.

It is highly probable that, if these two occurrences were known from more complete and more comparable material, it would be found that they should be specifically separated, but there is no valid basis for doing so at the present time. If the incisors are properly associated with the Benson specimen, it may become necessary to establish a separate genus for this form, differing from *Cupidinimus* in having grooved upper incisors and from *Dipodomys* in having rooted cheek teeth, in addition to other differences that may be discovered later. What the upper incisors of the Thousand Creek form were like, we do not know.

There are distinct resemblances of this species to *Microdipodops*, to which it is possible that it is related. The grooved incisors, high crowned but rooted teeth, the steep angle of the anterior end of the masseteric crest, the fact that P^4 is the largest of all the upper teeth, all would fit this genus as well as, or better than, *Dipodomys*. But *C. magnus* is much larger than *Microdipodops*. Of much greater significance is the fact that in the fossil, P^4 is definitely tending toward reduction of the two lophs, upon wear, to a single oval, whereas in *Microdipodops*, the two columns remain independent of each other, apparently throughout life (Merriam, 1891, p. 115). The two lophs of the lower premolar of *C. magnus* are much more independent of each other than is the case in *Microdipodops*, another character in which the resemblance is closer to *Dipodomys*. All specimens of *Dipodomys* show that the pattern of P_4 is retained much longer than is that of any other tooth, as appears to be the case in *C. magnus*.

The occurrence of *C. magnus* in the Benson beds indicates a short time interval between that formation and the Thousand Creek (fig. 1). The definite interval between the two formations, and the considerable distance between the two localities (see map, fig. 156) strengthens the possibility that the two forms would be separable on the basis of better and more complete material. This paper represents only the very early stages in correlation on the basis of heteromyids, as heretofore not sufficient material has been at hand to warrant any confidence in the results. It is very possible that quite exact correlations could be made if sufficient good material were available, as the heteromyids seem to have been evolving, in several different lines, at a fairly rapid rate throughout the later Tertiary and Pleistocene.

Dipodomys Gray, 1841

Synonymy:
MACROCOLUS Wagner, 1846.
PERODIPUS Fitzinger, 1867.
DIPODOPS Merriam, 1890.

Figs. 67-85; Schreber, 1846, Pl. 239E, fig. 3; Baird, 1857, Pl. 51, figs. 1a and e, 2f and g; Tullberg, 1899, Pl. 27, figs. 31-32; Grinnell, 1922, figs. J-P.

Diagnosis: Ricochetal form; highly inflated auditory region; cheek teeth hypsodont and ever-growing; tendency for thinning and breaking of the enamel on the buccal and lingual margins of the teeth, leaving only an anterior and a posterior blade in the more progressive species; metacone of P^4 blocks the median valley, uniting with both protocone and hypocone, so that the tooth has a U-shaped pattern, with the valley opening lingually; lophs of M^{1-2} unite lingually first; those of M^3 unite buccally; lophs of lower molars unite in a strong H-pattern; interparietal greatly reduced; zygomatic process of maxillary much expanded; deep pit at base of coronoid process, containing mandibular foramen; anterior end of masseteric crest at an angle of about 45°, ending in a strong process, which seems progressively to grow upward, enclosing part of the muscle; contact between navicular and calcaneum well developed; sometimes a cuneiform-calcaneal contact is present; tail tufted.

Range: Pliocene of Arizona; Pleistocene of California; Recent of western United States and Mexico (see map, fig. 156).

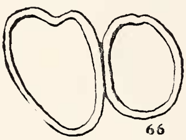
The upper premolar of *Dipodomys* has the same general pattern as that of *Microdipodops*, but the buccal position of the point of union between the lophs is brought about by the migration of the metacone, and not by that of the protocone, as in the Perognathinae. The tooth does not preserve the two distinct columns as long as in *Micro-*

dipodops. In some specimens, the protoloph appears to be two or even three cusped, suggesting a retention of the paracone, but this may be a secondary modification. All of the cusps are so crowded together that it is possible that only one cusp is present on the protoloph in all forms. If *C. nebraskensis* is ancestral to *Dipodomys*, any multiplicity of cusps in the protoloph of P^4 would have to be secondary, as there is only a single cusp in the Valentine form.

The lower premolar has a three-cusped metalophid and a two-cusped protolophid. The additional cusp has been developed in the middle of the posterior loph. In some specimens, at least, there is an anterior cingulum present in unworn teeth, extending from the two margins of the tooth, sometimes not quite meeting in the center. M_3 varies greatly. In some animals, it is five-cusped, lacking a hypostylid. In others, the hypostylid appears to be present. In some, the entire hypolophid is suppressed. In all, it is reduced. This is certainly a case of degeneration. There is a strong anterior cingulum, arising from the protostylid. In slightly worn specimens, the hypolophid may appear to be well developed. But in all such forms that were studied, the two crests that appeared to be metalophid and hypolophid were actually the anterior cingulum and the metalophid. Otherwise, the patterns of the teeth are very similar to those of *Cupidinimus.*

In the lower molars, the protoconid and hypoconid form the first point of union between the two lophs, giving the very characteristic H-pattern. In the upper teeth, the lophs of the first and second molars are normal, uniting lingually first, whereas those of the premolar and last molar unite first at the buccal side. In the third molar, this is due to the accentuation of the buccal cuspule of the metaloph, as in *Microdipodops* (fig. 30), which results in giving the tooth an outer wall of elevated ridges, surrounding a central lake, as in the Heteromyinae, although the result has been attained in a slightly different manner, and as an entirely parallel development.

In the upper deciduous premolar (fig. 67 and Baird, fig. 1e), the pattern is quite similar to that found in progressive species of *Perognathus*, but approaches even more closely to the conditions in *Liomys* and *Heteromys.* There are three transverse crests—an anterior one, formed of a single cusp; a central one with two cusps; and a posterior one with three cusps. Occasionally, as in *D. ordii richardsoni*, additional cusps may occur at the buccal margins of the two posterior crests, but the pattern is very uniform throughout the genus. The two posterior crests correspond to the two lophs of the permanent molar, from which they differ in that the point of union of the lophs is at the lingual, instead of the buccal, margin. In this respect the milk tooth is more primitive than the permanent one. The parts of the tooth correspond very closely to those in dP^4 of *Microdipodops* (fig. 32), but the tooth shows no sign of being surrounded by cingula as in that form, the anterior cuspule seeming to be merely an upgrowth from the anterior slope of the protoloph, as appears even more to be the case in *Heteromys* and *Liomys* (see below, figs. 131, 143). The buccal cuspules of *D. ordii richardsoni* appear unique in the family.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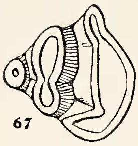
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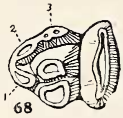
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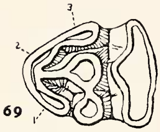
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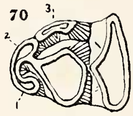
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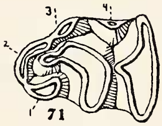
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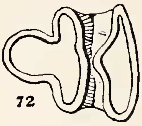
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FIG. 66. *C. magnus*, A. M. N. H. no. 21835, LP^4—M^1, × 10.
FIG. 67. *Dipodomys ordii richardsoni*, A. M. N. H. no. 7774, LdP^4, × 10.
FIG. 68. *D. m. merriami*, A. M. N. H. no. 6878, RdP_4, × 10.
FIG. 69. *D. o. richardsoni*, A. M. N. H. no. 7774, RdP_4, × 10.
FIG. 70. *D. merriami melanurus*, A. M. N. H. no. 32335-B, RdP_4, × 10.
FIG. 71. *D. agilis simulans*, A. M. N. H. no. 5057, RdP_4, × 10.
FIG. 72. *D. spectabilis*, A. M. N. H. no. 6814, RdP_4, × 10.

The lower milk molar is, however, much more variable. It is possible to work out a fairly complete series of evolutionary stages for this tooth within the few species of *Dipodomys* available for comparison. The most primitive type was found in *D. m. merriami* (fig. 68) and in *D. nitratoides*. In this type, the metalophid is formed of three cusps, the buccal one being obviously a hypostylid. The lingual half of the protolophid is formed by two large cusps, close together, which appear to be the protoconid and mesoconid. Between and anterior to these is another cusp, which seems to correspond to the anteroconid of dP_4 of *Perognathus* (fig. 25) and of P_4 of *Liomys* (fig. 130). Buccal to this and to the two main cusps of the protolophid is a series of two to four cingulum cusps, not yet greatly differentiated from the cingulum, whose lingual end attaches to the anteroconid. This tooth differs from dP_4 of *Microdipodops* in the more limited extent of the cingulum, and the greater association of the anteroconid with the protoconid and mesoconid (fig. 33). The next stage, as represented by *D. merriami melanurus* (fig. 69) and *D. ordii richardsoni* (fig. 70) involves a modification of the relationships of the mesoconid, so that it unites via a crest with a second and more buccal stylid (cusp No. 2). This seems to have been brought about by a buccad movement of the mesoconid. Otherwise, this type is similar to that described for *D. m. merriami*. In *D. agilis*, the mesoconid is moving still further buccad, apparently pivoting about the point where it meets the paraconid (fig. 71), and has almost established direct connection with the mesostylid. The primitive connection with the lingual margin of the cingulum is still retained, though reduced, so that an enamel lake is developed in front of the mesoconid. The cingulum cusps are better developed in this species than in any other studied, an additional cuspule appearing in the valley between the protolophid and metalophid. The number of stylids varies somewhat in different species, and their mutual homologies are difficult to determine, but an attempt has been made in figs. 68-71 to establish as exact a homology as possible. Another variation in pattern is represented by *D. spectabilis* (fig. 72). Unfortunately, no unworn specimens of this type were seen, so its pattern can not be accurately determined. This series of modifications in the deciduous teeth of *Dipodomys*, especially in the lower one, has apparently been developing in a manner all its own, nearest to what has occurred in *Microdipodops* and *Heteromys*, but still fundamentally distinct from both.

In its habitus features, both skull and skeleton of *Dipodomys* present a very close parallel to *Microdipodops*. There is the same inflation of the bullae, the same hypsodonty of the cheek teeth, although it has been carried further in the kangaroo rats, which have lost all trace of roots. The reduction of the enamel, to be discussed below in the case of the individual species, is without parallel in *Microdipodops*, but is very close to, if not identical with, what has taken place in the related Geomyidae, although occurring at a later time. The expansion of the maxillary, antero-posteriorly, over the anterior portion of the orbit, uniting with the lacrymal and frontal, is essentially unique among heteromyids, although it appears to be foreshadowed in *Cupidinimus.* The temporal fossa, making a notch in the postero-lateral margin of the parietal, is entirely absent in this genus, and the lateral process of the parietal, separating the squamosal from the mastoid, is very short. The compression of the interparietal has proceeded in much the same way and to much the same extent as in *Microdipodops.* An important feature is that the bullae, although nearly as much expanded as in *Microdipodops* and more so than in *Perognathus*, essentially do not expand below the level of the grinding surface of the upper cheek teeth. Cervical fusion has proceeded as in *Microdopodops* and other saltators (Hatt, 1932, pp. 637-641). There are median ventral foramina in the caudal vertebrae, distinguishing *Dipodomys* from *Microdipodops* and other Perognathines.

The hind legs of *Dipodomys* have been considerably elongated, the revised intermembral index averaging 36 (see Table V). This is parallel to the similar modifications in *Microdipodops* and the Dipodidae. Locomotion, in *Dipodomys*, is always ricochetal except when the animal is merely crawling along. The general effect of the ricochet is much like that of a child on a "pogo-stick," or the rebound of a ping-pong ball.

The most important feature in the pes of *Dipodomys* is the calcaneal-navicular contact, otherwise occurring, among heteromyids, only in *Cupidinimus.* In all the specimens of kangaroo rats that I have studied, this contact is clearly developed. Grinnell gives illustrations of the tarsus of seven specimens of *Dipodomys*, representing five species (1922, figs. J-P). All but one of these (fig. M, a ♀ *D. heermanni*) show the calcaneal-navicular or calcaneal-cuneiform contact. This one appears to have an astragalar-cuboid contact. It is certain, however, that this is a very rare occurrence in *Dipodomys.*

As in all ricochetal forms, digits II-IV tend to converge at their distal ends. Another ricochetal adaptation is the progressive reduction and loss of the hallux in some species, paralleling the jerboas. This character was formerly considered the generic distinction between *Dipodomys* and *Perodipus*, but as all gradations have been found between the two extremes, and as the absence of the hallux is not constant, *Perodipus* is now generally considered as a synonym of *Dipodomys.*

At this point it may be well to review what is known of the ancestry of *Dipodomys.* Besides needing a form that would belong to the

Dipodomyinae, one would expect that a middle or late Tertiary ancestor would be developing the ricochetal habitus; the auditory region would not be greatly swollen, but the mastoid would be enlarging; the anterior lip of the external auditory meatus would be slightly swollen; the cheek teeth would be high crowned but rooted, with the enamel complete; the metacone of P^4 blocking the median valley and moving into close relationships with the protocone; the interparietal much less reduced than in the living *Dipodomys;* the zygomatic process of the maxillary beginning to expand; and the calcaneum not articulating so broadly with the navicular. In all of these characters, *Cupidinimus nebraskensis* is an exact fit for the specifications. The ricocheting was clearly beginning; the auditory region is relatively little swollen, though more so than in most species of *Perognathus;* the anterior lip of the external auditory meatus is expanding; the interparietal is similar in configuration to that of the more progressive species of *Perognathus;* the cheek teeth are high crowned, rooted, and with complete enamel; the metacone of P^4 begins to block the median valley; the zygomatic process of the maxillary is beginning to expand; and, lastly, the foot structure and other points indicate without doubt that this form belongs in the Dipodomyinae. The fact that the specimens of *C. nebraskensis* were found in large numbers in sand deposits may indicate a similar type of habitat and a similar location of burrows. It is true that the upper incisor is grooved in *Dipodomys* and smooth in *Cupidinimus*, but the grooved type must have been derived from the smooth one at some time. Of course, this would make necessary the postulation of the development of the grooved type of incisors at least once in each subfamily, independently of each other, but the extreme amount of parallelism represented in other characters makes this entirely conceivable, especially as grooved incisors have been independently developed in many families of rodents—as the Heteromyidae, Geomyidae, Castoroididae, Cricetidae, Hydrochoeridae, and others. The common ancestor of the Perognathinae and Dipodomyinae, then, could not be found later than the Lower Miocene, since the middle Miocene *Mookomys* already has grooved incisors, unless we have another instance of reversal of evolution, which, of course, is perfectly possible.

While *Dipodomys* appears definitely to be derivable from *Cupi-*

dinimus as far as the structure of the two forms is concerned, there are, nevertheless, considerable differences between the two genera. Hence, it might be argued that *Dipodomys*, appearing as early as the Upper Pliocene, has not had sufficient time to have evolved from the Lower Pliocene *Cupidinimus*. But it must be remembered that *Dipodomys* is essentially a desert form, and that its desert adaptations could not develop before the deserts did, but that once there were such conditions available for the genus, the evolution might well proceed with great rapidity. It seems well demonstrated that an animal which enters an entirely new facies, with little or no competition, will make great progress in a very limited amount of time. Thus, it seems possible that *Dipodomys* may be descended from *C. nebraskensis*, and it is quite probable that the Late Miocene to Early Pliocene ancestor of *Dipodomys* will be found to fall within the limits of *Cupidinimus*.

In the discussion of the species entered into below, only the fossil species and such recent ones as have been available to me in the collections of the American Museum were considered. The object in studying the recent forms in detail has been twofold: first, to determine with what recent species the fossils might be most closely united, and second, to determine whether dental characters could be used to distinguish the living species from each other. Having been successful to varying degrees along both lines, the results are included below. A key of these species, for identification by means of the cheek teeth, has been added, which could probably be extended to include other species on further study. The American Museum collections contain only one species for each species-group listed by Miller (1924), excepting the *D. merriami* group, which is represented by two species. Hence, it is possible that the characters listed below are those of the species-groups and not of the individual species. No significant differences were noted between the various subspecies of a particular species, except for the variation mentioned above, in the deciduous premolar in *D. merriami*. In part, at least, this may be due to the small series of specimens available showing unworn teeth, and the limited amount of time available to study these forms. As published figures of the teeth of *Dipodomys* are conspicuous by their absence, several are included below. The only figure of deciduous teeth with which I am familiar is that in Baird, 1857.

KEY TO THE SPECIES OF *Dipodomys* IN THE AMERICAN MUSEUM, BASED ON TOOTH STRUCTURE.

1. Crowns of teeth persist an appreciable time after all the teeth have been erupted.
   a. Enamel complete throughout life.
      i. small size .... *compactus*
      ii. medium size .... †*minor*
   b. Enamel interrupted slightly after much wear.
      i. medium size .... *nitratoides*
   c. Enamel interrupted slightly after little wear.
      i. medium size .... *merriami*
2. Crowns of the teeth destroyed by or shortly after the time the last tooth has been erupted.
   a. Enamel complete throughout life.
      i. medium size .... †*gidleyi*
   b. Enamel breaks small, developing late.
      i. unworn teeth with oval ends .... *ordii*
      ii. unworn teeth with square ends .... *agilis*
   c. Enamel breaks small to medium in size, with an appreciable period before they show on the grinding surface.
      i. unworn teeth with square ends .... *heermanni*
      ii. unworn teeth with oval ends .... *spectabilis*
   d. Enamel breaks very large, developing very early.
      i. large. Enamel thick .... *deserti*

The above arrangement differs strikingly from that given by Grinnell (1921), who lists the species-groups in order of increasing specialization as *heermanni*, *spectabilis*, *phillipsii*, *merriami*, *ordii*, *compactus*, *agilis*, *microps* and *deserti*. The chief point of agreement between the two arrangements is that both place *D. deserti* as the most specialized. This divergence, however, should cause no surprise, as there is no known reason why the species that are the most specialized in one character should be equally advanced in another, although one may be likely to jump to that conclusion. The above list, then, can merely be considered to represent what appears to be the classification on the basis of increasing specialization of tooth structure alone.

Dipodomys minor Gidley, 1922

Fig. 73 and Gidley, 1922, Pl. 34, figs. 16, 16a.

Holotype: U. S. N. M. No. 10499, right lower jaw with P_4, from the Benson Pliocene of Arizona. Referred specimen, A. M. N. H. No. 27790, from the Curtis Pliocene of Arizona, right lower jaw with P_4—M_1.

Diagnosis: Anterior loph of P_4 much larger than posterior; enamel complete on all portions of P_4—M_1, without any trace of a break; M_1 much wider than in *D. compactus*, but no longer; M_3 more reduced than in *D. chapmani;* jaw more slender than in that form.

The American Museum specimen adds something to our knowledge of this, one of the earliest known forms which can be referred to the genus *Dipodomys*. What we know of it certainly allows it to be classed as one of the most primitive species of the genus, in that it has no signs of having developed the enamel breaks so characteristic of the more progressive species—nor is there any trace of grooving on the sides of the teeth, the initial stage in the development of interrupted enamel, except very far down, well below the gums. And the teeth of this specimen are well worn. The alveoli of M_{1-2} are of about equal width, and are wider than is that of P_4. This is one difference from *D. compactus*, in which M_2 is definitely smaller than M_1, and of about the same width as P_4, the fossil representing a more primitive stage than the living species. The wear has proceeded to the point where all trace of the crown pattern has been lost on the molar, the cusps of the premolar have been entirely worn away, and the invaginations are becoming rapidly destroyed. The premolar is quadrangular. The invaginations of this tooth would be entirely destroyed before the slight grooves on the sides of the posterior loph came near the grinding surface. The rear end of the jaw is broken away, and the base of the molar is clearly shown. It is of the typical, open, ever-growing type found in the living species, and shows no traces whatever of roots. The symphysis is short. The masseteric crest is simple, without the overgrowth to be found in *D. spectabilis* and other forms. The anterior end of the crest forms a much more prominent knob than in *D. spectabilis*, much as it does in *D. compactus*. There is no evidence of any grooving in the lower incisor.

D. minor, then, is one of the most primitive known species of *Dipodomys* with regard to the length of the symphysis, the characters of the masseteric crest, and the absence of interruptions of the enamel. Its relationships seem to be closer to *D. compactus* than to any of the other recent forms studied.

D. gidleyi n. sp. (Fig. 74.)

Holotype: A. M. N. H. No. 21848, right lower jaw, with P_4 to M_3 in fragmentary condition, collected by J. W. Gidley, March 10, 1924, from the *Stegomastodon arizonae* excavation, Curtis Flats, near

Benson, Arizona. Some associated limb bones appear to belong to the same individual.

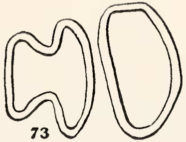
Diagnosis: Enamel complete throughout life; protolophid of P_4 narrower than metalophid but longer; P_4 narrower than M_{1-2}; M_3 not greatly reduced.

I take great pleasure in naming this species after Dr. James W. Gidley, in recognition of his extensive work in vertebrate paleontology in general, and on the classification of rodents in particular. The name is rendered especially appropate in that this specimen was collected by Dr. Gidley himself.

Although the crowns of the teeth of the holotype are considerably broken, the lower portions, in the alveoli, are essentially complete, and permit the reconstruction of the pattern as given in fig. 74. Even if the molars had not already attained the pattern shown, they certainly would acquire it after further wear. This species is quite distinct from the contemporary *D. minor.* It does not have the groove between the protoconid and mesoconid of P_4, even though the holotype is much less worn than is either known specimen of *D. minor.* The protolophid is proportionately smaller than in that species, while the metalophid is longer. M_1 is considerably wider than the premolar, and M_2 slightly so, this last being a distinction from *D. minor* and *D. compactus.* M_3 is less reduced than either of those species. All of these characters represent approaches to *D. ordii*, to which *D. gidleyi* seems very possibly related.

The sides of the teeth show no traces of grooves representing the initial stage in interruption of the enamel, which is definitely a primitive character. There appears to have been a rapid erosion of the crowns of the teeth, as no trace of the pattern appears to be preserved on any of the molars, even though the premolar has not been long in use. The posterior part of the jaw is unfortunately not preserved, but there apparently was not as deep a pit beside M_3 as in *D. ordii.* The masseteric crest is peculiar in its configuration, being horizontal in the posterior section, sloping upward at about 45° in the center, and then flattening out again anteriorly, a feature which I have not observed in any other heteromyid.

The measurements of the limb bones seem to be about ten percent smaller than the corresponding measurements of *D. ordii luteolus.* The great trochanter extends but little beyond the head. The tibiofibula, as far as can be told from the distal half, is very similar to that of *D. ordii*, though proportionately larger than is the femur. The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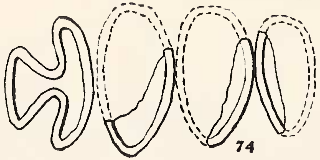
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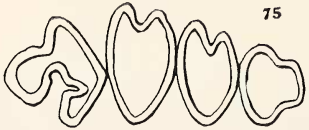
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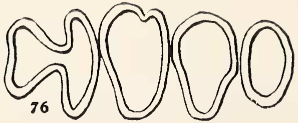
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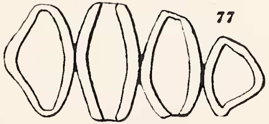
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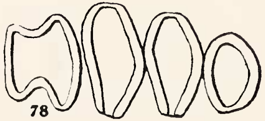
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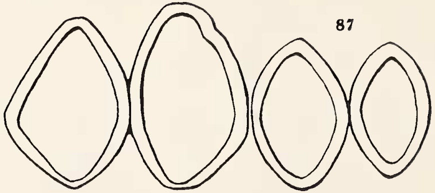
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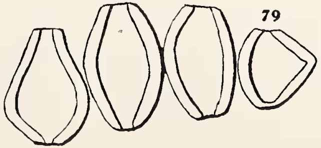
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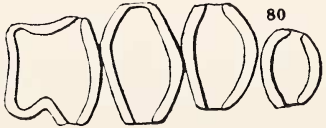
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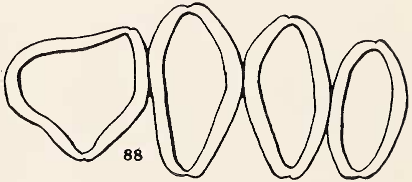
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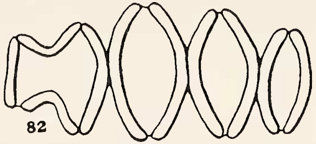
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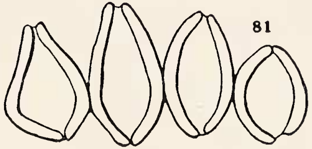
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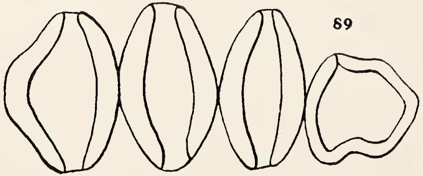
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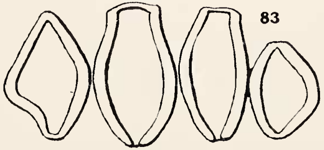
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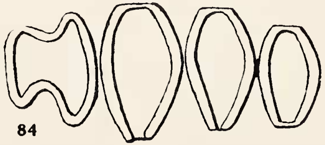
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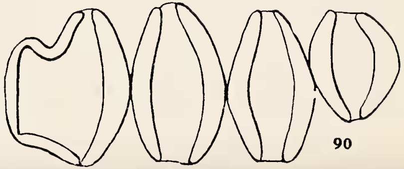
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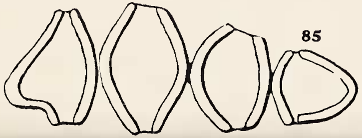
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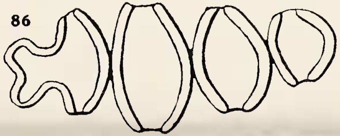
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distal two thirds of the humerus is preserved, and is essentially the same size as is that of *D. ordii*, which would indicate less reduction of the fore-limb, and therefore a lesser ricochetal adaptation. The olecranon and half of a long, slender metatarsal are also associated with this specimen.

While this form differs from *D. ordii*, most of the differences appear to consist in the fossil being more primitive than the Recent species, which is not overwhelmingly astonishing. It certainly suggests very strongly that it either is ancestral to *D. ordii*, or else is very close to such a position, and is so indicated in the phylogenetic chart (fig. 1).

Dipodomys compactus True, 1884 (Figs. 75-76.)

This is definitely the most primitive living species, considered from the point of view of the tooth pattern alone, that was available to me for study. The enamel is complete throughout life, as far as is determinable from the material in the American Museum collections. The teeth are erupted fairly close to the same time, and the crowns are relatively well developed, as traces of the pattern may be seen on all of the teeth at the same time. The posterior lophs of the upper molars are definitely shorter than are the anterior lophs, a condition especially well marked on the third molar, where the metaloph is about half the length of the protoloph (fig. 75). The metaloph of M^3 is formed of two distinct cusps, the entostyle being two or three times

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EXPLANATION OF FIGURES

FIG. 73. *D. minor*, A. M. N. H. no. 27790, RP$_4$—M$_1$, × 10.
FIG. 74. *D. gidleyi*, A. M. N. H. no. 21848, RP$_4$—M$_3$, × 10.
FIG. 75. *D. compactus*, A. M. N. H. no. 2732, LP^4—M^3, × 10.
FIG. 76. *D. compactus*, A. M. N. H. no. 2732, RP$_4$—M$_3$, × 10.
FIG. 77. *Dipodomys nitratoides*, A. M. N. H. no. 13828, LP^4—M^3, × 10.
FIG. 78. *D. nitratoides*, A. M. N. H. no. 13828, RP$_4$—M$_3$, × 10.
FIG. 79. *D. merriami*, A. M. N. H. no. 6824, LP^3—M^3, × 10.
FIG. 80. *D. merriami*, A. M. N. H. no. 6824, RP$_4$—M$_3$, × 10.
FIG. 81. *D. ordii luteolus*, A. E. W. no. 1302, LP^4—M^3, × 10.
FIG. 82. *D. ordii luteolus*, A. E. W. no. 1302, RP$_4$—M$_3$, × 10.
FIG. 83. *D. agilis*, A. M. N. H. no. 4577, LP^4—M^3, × 10.
FIG. 84. *D. agilis*, A. M. N. H. no. 4577, RP$_4$—M$_3$, × 10.
FIG. 85. *D. heermanni*, A. M. N. H. no. 13834, LP^4—M^3, × 10.
FIG. 86. *D. heermanni*, A. M. N. H. no. 13834, RP$_4$—M$_3$, × 10.
FIG. 87. *D. spectabilis*, A. M. N. H. no. 35035, LP^4—M^3, × 10.
FIG. 88. *D. spectabilis*, A. M. N. H. no. 35035, RP$_4$—M$_3$, × 10.
FIG. 89. *D. deserti*, A. M. N. H. no. 2598, LP^4—M^3, × 10.
FIG. 90. *D. deserti*, A. M. N. H. no. 2598, RP$_4$—M$_3$, × 10.

as large as is the metacone. The lophs of this tooth unite first on the buccal side, as is the case in the premolar. The other two molars unite first on the lingual side. The anterior loph of M^1 is the widest of the whole upper series. From here caudad, each successive crest is shorter than the preceding one. Crenulations are sometimes present in the enamel of $M\frac{1}{1}$. P_4 is quadrate, as in all species studied except *D. spectabilis*. No grooves are present in the enamel on the sides of the teeth, so that there is apparently not even any thinning of the enamel, as far down on the teeth as can be seen on any specimen available. This is a more primitive situation than that existing in *D. minor*. There is certainly no trace of any thinning in the crown view of the teeth, thus differing from most post-Tertiary species of *Dipodomys*. There is a pit with the mandibular foramen at the bottom between M_3 and the base of the coronoid process.

In the skull, the mastoid region is less inflated than that of any of the other species of *Dipodomys* studied, approaching closely to such forms of *Perognathus* as *P. apache* (see Table IV). *D. compactus* appears very close to *Cupidinimus* in the general proportions and arrangement of the auditory region, and is probably even closer to *D. minor*. The interparietal is wider in *D. compactus* than in the other species of *Dipodomys* studied, reaching 3.75 mm.

On the basis of tooth structure and amount of inflation of the auditory region, this species must be considered as one of the most primitive, if not the most primitive, of the living species of kangaroo rats. The general aspect of the teeth appears to indicate close relationships with *D. minor* of the Upper Pliocene, of which it may be a descendant.

Dipodomys nitratoides Merriam, 1894 (Figs 77-78.)

In this species, also, the eruption of the teeth is sufficiently nearly simultaneous so that the crown patterns of the whole series can be seen in the same animal. The enamel develops small breaks after a considerable period of wear. They appear first on the buccal margins of the upper molars. $M\frac{3}{3}$ are subtriangular. The other cheek teeth are much compressed antero-posteriorly. The anterior surface of the lower incisor is rounded. The masseteric ridge of the mandible is small, and slopes steeply upward. The symphysis ends at the level of the mental foramen. The interparietal is 1.58 mm. wide. The skull index is 67.5 (See Table V).

Dipodomys merriami Mearns, 1890 (Figs. 79-80.)

This species is of medium size. The teeth are all erupted close to the same time, and the crown patterns persist for an appreciable period, as in *D. minor* and *D. compactus*, so that the pattern is visible on all the teeth at once. The enamel, however, soon develops interruptions at both buccal and lingual margins. In P_4, there are four enamel breaks, at the buccal and lingual margins of both lophs. The protolophid and metalophid are subequal in length, a primitive character. P^4 to M^2 are all almost the same size, with little difference in any dimensions. The masseteric crest is nearly horizontal, and terminates anteriorly in a knob. The anterior surface of the lower incisor is rounded. A small knob is present at the postero-inferior border of the infra-orbital foramen, for the attachment of the edge of the masseter. The interparietal is 1.9 mm. wide and the skull index is 65.4.

Dipodomys ordii Woodhouse, 1853 (Figs. 81-82.)

The patterns of the teeth of this species disappear rapidly, though the premolars erupt before the pattern is entirely destroyed on the molars, which is probably essentially the situation in *D. gidleyi*. This species may be distinguished from the two following ones by the fact that the teeth are oval, not having square ends. The interruptions of the enamel develop rather late. P^4 and M^1 are almost of equal size (fig. 81). The lophs of M^{1-2} are united lingually before the tooth has been erupted, indicating no valley at all between the protostyle and the entostyle, which may be a primitive condition, indicating lack of subdivision of the cingulum, but seems more likely to be secondary. The metalophid of P_4 is definitely shorter antero-posteriorly than is the protolophid (fig. 82). There are four enamel breaks in this tooth, although the two at the ends of the metalophid do not develop until quite late in life. The lower incisor has a flat anterior face in most specimens, though occasionally it is rounded, especially at the lateral edge. The symphysis is short, but extends to below the masseteric ridge, which is folded up over the insertion of the masseter, and slopes upward, sharply, at its anterior end. The interparietal averages 2.86 mm. in width, and the skull index is 62.3.

Dipodomys agilis Gambel, 1848 (Figs. 83-84.)

As in *D. heermanni*, though to a lesser degree, this species has square buccal ends on the first and second upper and lower molars. The break in the enamel, which develops quite late in life, even though the crowns disappear with great rapidity, apparently appears first on the buccal side of the lower teeth and the lingual side of the upper ones. The third molars are proportionately quite large. The anterior surface of the lower incisors is rounded. The masseteric ridge slopes upward anteriorly, and has folded up over portions of the masseter, which are squeezed between the crest and the body of the mandible. The interparietal is 1.42 mm. wide, and the skull index is 61.1.

This species is also known as a fossil, occurring in the Upper Pleistocene deposits of Rancho La Brea. Dice (1925) considers the fossils indistinguishable from *D. agilis agilis*. This is the only living species of kangaroo rats that has as yet been reported as fossil, probably correlated with the fact that most of the better known Pleistocene localities are outside the range of *Dipodomys* (see map, fig. 156).

Dipodomys heermanni LeConte, 1853 (Figs. 85-86.)

The interruptions of the enamel in this form develop after a fair amount of wear. The most striking peculiarity is the square buccal ends of the first and second molars. The crown patterns of the molars are destroyed before the premolars are erupted. The molars taper linguad. In slightly worn teeth, the enamel covers the square buccal ends as a thin band, which persists for a considerable period of time. The teeth tend to be compressed, antero-posteriorly. M^3 is as long as are either M^1 or M^2. The enamel interruptions develop first on the buccal side of M^{1-2} and the lingual side of M_{1-2}. The masseteric ridge is short, nearly horizontal, and folded up over the muscle for about half a millimeter. The symphysis reaches the anterior end of the masseteric ridge. The anterior face of the lower incisor is rounded. The interparietal is usually wide, averaging about 2.7 mm., but in some specimens it is very narrow, reaching as little as 0.9 mm. in one animal. The skull index averages 62.7. The pit between M_3 and the base of the coronoid is extremely shallow, although it has the foramen at its bottom, as usual.

Dipodomys spectabilis Merriam, 1890 (Figs. 87-88.)

This species is one of the two of large size that were studied. The pattern is confined to a very small part of the crown, and is worn away with great rapidity, being destroyed on one tooth before the next is erupted. The enamel breaks are rather slow in developing, and are not very large when they do appear. The protolophid of P_4 is quite small, although two-cusped, so that the tooth is triangular in outline (fig. 88), paralleling the modification described above as occurring in *Perognathus*. Correlated with this, only two enamel breaks occur, those in the metalophid. This is the longest tooth, antero-posteriorly, in either jaw. M_{1-2} are wider than P_4, while P^4 is wider than M^2 (fig. 87). M^3 is slightly reduced. The first appearance of enamel breaks is on the buccal side of the upper teeth and the lingual side of the lowers. The increase in size of the breaks, as the tooth wears away, is slow, with practically no visible difference in their size from grinding surface to alveolus. The anterior face of the lower incisor is flat, and has a distinct, though shallow, groove near its center, in some specimens. This represents an independent acquisition of grooving of the lower incisors, paralleling that in *Hydrochoerus*, and not found in other heteromyids. As apparently it is an individual variation, it shows the lack of fundamental significance of such a modification among rodents. Whether a shallow groove represents an initial step toward the development of a deep groove, or whether it is an independent mutation, can not be determined. Other than the depth of the grooves, there is no significant difference visible between the groove of the upper, and that of the lower, incisors.

The masseteric ridge is nearly horizontal, and has grown dorsad, enclosing a narrow space between itself and the mandible, into which is crowded part of the insertion of the masseter. The anterior end of the crest is about a third of the way from the alveolus of P_4 to that of the incisor. The infraorbital foramen seems unusually far forward. The interparietal is 2.4 mm. wide and the skull index is 64.3.

Dipodomys deserti Stephens, 1887 (Figs 89-90.)

This species is without any doubt the most highly specialized of any *Dipodomys* that I have studied, and is the only form as to whose relative specialization both Grinnell (1921) and the present author are in agreement. The bullae are huge, and frequently meet in the center of the dorsal surface of the skull, completely hiding the interparietal and supraoccipital from sight, and are almost as much inflated as in *Microdipodops*. The skull index is 66.0, approaching the 68.7 of the latter form. The maximum width of interparietal seen in any specimen was 0.3 mm., and the average was but 0.12. The supraoccipitals are inflated as well as the tympanics and the mastoids. There are strong knobs for the masseter postero-ventrad of the infraorbital foramen. The enamel is very thick in this species, reaching a maximum of 0.30 mm., at least 20% greater than in any other species studied. M^{1-2} are subequal (fig. 82). M^3, although narrow, is almost as long as P^4, and is longer than any other tooth in either jaw. M_{1-3} are nearly uniform in length, but M_3 is considerably narrower transversely (fig. 90). There are no grooves at the sides of the teeth, because the enamel plates are too far apart to leave a notch between themselves as in other species. P_4 is the last tooth to develop interrupted enamel. These interruptions begin sooner in this species than in any other, and increase in size with greater rapidity. The breaks appear to develop lingually first in the upper teeth and in P_4, but buccally first in M_3. The crown patterns of the cheek teeth are lost with extreme rapidity. The lower incisors are without sulci, and are slightly rounded on their anterior face. The masseteric ridge is high, folded up over the masseter, and slants upward anteriorly.

In habitus characters, this species appears to approach closer to *Microdipodops* than does any other member of the genus, although there is still as great a gap as ever between the two forms in heritage characters. The close parallelism which has developed is probably due to both being extreme desert adaptations, and living in very similar habitats, with similar habits, where they would both be affected by the same factors of natural selection, operating on identical, or similar, series of mutations. *D. deserti* is quite widely separated from the other species of kangaroo rats, and probably represents an independent line since well into the Pliocene.

It may be noted that, in these last two species of *Dipodomys* the crowns are worn away with greater rapidity than in any of the other species. As these are the two largest species studied, there is a suggestion of some connection between size and the rate of destruction of the teeth. In *Dipodomys*, the occlusal part of the crown has not partaken of the elongation which has affected the rest of the tooth.

As the teeth are larger, absolutely, in the larger species, it may be that this represents a recent increase of size, and that the occlusal part of the crown did not share in it, thus becoming an even smaller proportion of the crown than before. If this were the case, it would disappear with greater rapidity than before. As *D. deserti* has the most specialized dentition in other respects, it may have advanced beyond the other forms in the reduction of the occlusal part of the crown. Or, there may be a mechanical cause for the rapid wearing away, in that the larger animals eat tougher food and get a larger quantity of sand grains into their mouths, which could greatly increase the rate at which the teeth were worn away. The pulps may grow faster in these forms, forcing the teeth out at a more rapid rate, and thus requiring that they be worn off at an equal rate. If the teeth were not worn off with sufficient rapidity, on this assumption, the animal would soon be unable to close his mouth, and would starve to death. Such a happening would be unlikely to become established as the general rule in a species. Whatever the cause, there seems little doubt that the larger the kangaroo-rat, the more rapid is the wearing away of the crowns of the teeth.

SUBFAMILY HETEROMYINAE Coues, 1875

Lophs of lower premolars first unite, when worn, at the buccal side, next at the lingual side; stylids progressively present on P_4, developing at any point on the tooth; lophs of upper premolars unite first at the lingual side, next at the buccal; protoloph of P^4 formed of more than one cusp; lophs of upper molars always, and of lower molars usually, unite at the two ends, surrounding a central basin; external cingulum of lower teeth migrates onto anterior side, and internal cingulum of upper teeth migrates onto posterior side, developing a secondary connection with the middle of the adjacent loph, giving a Y-shaped crest; cheek teeth rooted but progressively high crowned; in the hypsodont forms, the whole crown takes part in the increase, so that the pattern is preserved for a long time; upper incisors broad, and either smooth or with shallow sulci; two pairs of pits for the pterygoid muscles; ethmoid foramen present in dorsal part of orbit; bullae never reach level of grinding surface of upper cheek teeth; median ventral foramina present at anterior end of centra of caudal vertebrae; masseteric crest ends behind rather than above mental foramen; astragalo-cuboid articulation; fourth metatarsal longer than third; habitat ranges from semiarid, partially wooded regions to humid, heavily forested areas; locomotion predominantly scampering, occasionally subricochetal.

Genera: Proheteromys, Peridiomys, Diprionomys, Heteromys and *Liomys.*

Range: Miocene? of Colorado; Miocene of Florida, South Dakota, Nebraska and Oregon; Pliocene of California and Nebraska; Pleistocene of Yucatan; Recent of Central America and northern South America (Map. fig. 157).

Proheteromys Wood, 1932

Genotype: P. floridanus Wood, 1932.

Diagnosis: Cheek teeth bilophodont and in about the same stage of development as in *Mookomys*, and likewise based upon a primarily sextitubercular pattern; upper incisors asulcate; heteromyine pattern developing in cheek teeth; P_4 quadritubercular; posterior cingula on lower and anterior cingula on upper teeth.

Lower Miocene of South Dakota, Middle Miocene of Florida and Middle Miocene? of Colorado.

The genus represents the most primitive stage known which can definitely be included in the Heteromyinae. *P. magnus* from Florida is more specialized than the other species, heading toward *Heteromys*, in that it has a more progressive development of the Y-pattern (see below, p. 168) and a greater height of crown. *P. parvus* appears to represent an aberrant side line, due to its exceptional development of the posterior cingulum of the lower molars—cingula which do not appear among heteromyids other than in this genus. Probably none of the known species of the genus are directly ancestral to any known later forms, but *P. parvus* and *P. magnus* are strikingly suggestive of *Peridiomys*, and *P. magnus*, as far as we know it, seems definitely tending toward *Heteromys*, in the strongly developed Y-pattern, which has already reached a more advanced condition than is to be found in *Liomys*. As the upper teeth of *Heliscomys* have posterior, and the lower teeth have anterior, cingula, while the cingula are on the other ends in *Proheteromys*, it is possible that the former genus is not ancestral to the latter. But, in most characters, the two are similar, and *Heliscomys*, if not ancestral to the Heteromyinae, is not far removed from such a position.

Proheteromys floridanus Wood, 1932

Figs. 91-92; Wood, 1932, figs. 24-25.

Holotype: F. S. G. S. V-5329.

Diagnosis: Teeth in almost as primitive condition as in *P. parvus* (see below), except that P_4 consists of two crescentic lophs, whose ends are directed toward each other, surrounding a central basin; antero-posterior valleys between cusps almost as deep as median valley in all teeth; Y-pattern not shown on either holotype or paratype; no posterior cingula visible on lower molars of known specimen.

Middle Miocene of Florida.

This species is more progressive than *Heliscomys*, and somewhat more so than *P. parvus* (=*Mookomys parvus* (Troxell), Wood 1931) from Colorado, in that the lower premolar, while based on a quadritubercular pattern, thus differing from *Heliscomys*, consists of two concentric lophs, surrounding a central basin. *P. parvus* is much more cuspidate, the individual cones being essentially distinct entities. Part of the difference is one of wear, but even if *P. parvus* were worn to the same degree as is the holotype of *P. floridanus*, the lophs would not be so well developed. This tooth in *P. floridanus* is more rectangular and more elongate antero-posteriorly, representing advances over the more primitive subtriangular shape represented in *P. parvus*. An anterior cingulum seems to be developing on the upper molars of *P. floridanus*, which is probably a point of resemblance to *P. parvus*, although it is not so clearly shown as is the posterior cingulum in the lower teeth of the latter species. *P. floridanus* shows definite resemblances to *Liomys*, but most of these appear to be primitive heteromyine characters retained by both forms. But the ancestor of *Liomys* would seem, at present, to be likely to fall within the limits of this genus, and would certainly resemble *P. floridanus* more than it would any other known species. The only other fossils which have any close similarity to *Liomys* are the species of *Peridiomys*, which have established themselves as an aberrant line, having developed the H-pattern in the lower molars. *Peridiomys* is very likely descended from a form close to, but probably not identical with, *Proheteromys floridanus*, as it seems improbable, on geographic grounds, that a species of small rodents living in Florida should be actually ancestral to a genus living in Oregon and Nebraska, or to one living in Central and South America.

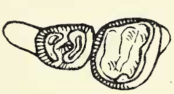

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FIG. 91. *P. floridanus*, F. S. G. S. V-5329, Holotype, LP$_4$—M$_1$, × 10. After Wood, 1932.

FIG. 92. *P. floridanus*, F. S. G. S. V-5330, RM^1, × 10. After Wood, 1932.

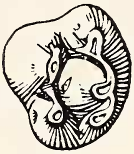
P. magnus Wood, 1932

Figs. 93-96; Wood, 1932, figs. 26-29.

Holotype: F. S. G. S. V-5332; paratypes, F. S. G. S. V-5333 and 5334.
Diagnosis: Size large; progressively lophodont; roots greatly elongate; posterior cingulum slightly developed in lower teeth; Y-pattern strongly foreshadowed.

Middle Miocene of Florida.

P^4 is quinquecuspidate, with two cusps in the protoloph, the inner apparently being a protostyle, which removes this species from possible relationship to the other subfamilies of heteromyids, in which the protoloph of P^4 is formed from the protocone alone. An incipient lingual movement of the hypocone, causing it to reach as far lingually as does the entostyle, is developing the first stages of the J-pattern so clearly shown in *Heteromys* (fig. 93, and below, fig. 133). This J-pattern is caused by the lingual margin of the entostyle uniting with the lingual margin of the hypocone, as the tooth is worn, so that the metaloph becomes J-shaped. In the lower molars (fig. 94-95), the similar buccal movement of the protoconid toward the protostylid has made a deep fold between these two cusps, and caused a migration of the external cingulum to the anterior side of the tooth, where it becomes an anterior cingulum. A result is to give the loph the shape of a Y, whence it is referred to as the Y-pattern. This migration is definitely beginning in *P. magnus*, though not yet completed. At the same time, the buccal movement of the protoconid, as well as the crowding due to the presence of the protostylid on its anterior face, has caused a shift in direction of the main axis of the meta-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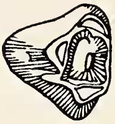
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FIG. 93. *P. magnus*, F. S. G. S. V-5332, Holotype, LP^4, × 10. After Wood, 1932.

FIG. 94. *P. magnus*, F. S. G. S. V-5333, LM_2, × 10. After Wood, 1932.

FIG. 95. *P. magnus*, F. S. G. S. V-5334, RM_3, × 10. After Wood, 1932.

FIG. 96. *P. magnus*, F. S. G. S. V-5336, LdP^4, × 10. After Wood, 1932.

lophid, so that there is a noticeable bend in its center, between the protoconid and the metaconid. This is very definitely foreshadowing the sharp change of direction to be found in *Heteromys*. The posterior cingulum of M_2 seems to be either in an incipient stage of development, or else is being lost by this species,—which, it is impossible to determine, although the former seems intrinsically the more likely.[5a] The tooth identified by Wood (1932, p. 48) as RM^3 seems, on further study, more probably to be RM_3. There is a strong incipient Y-pattern in the anterior loph, and no trace of anything like a posterior cingulum, or anything else which might have given rise to the posterior loph of M^3 of *Heteromys*. As the Y-pattern is typically developed in the anterior loph of the lower, and posterior loph of the upper, molars, in the Heteromyinae, and as the two teeth are otherwise likely to be very similar in a given animal, this tooth is now considered to be M_3. The tooth listed by Wood as "Heteromyid gen. et sp. indet." (fig. 96, and Wood, 1932, fig. 29, p. 48) probably represents a deciduous premolar of *P. magnus*, by analogy with the deciduous premolars of *Perognathus*, to which it bears a considerable resemblance (figs. 20-22, and above, p. 101). It is interesting to observe that in the Middle Miocene, the deciduous premolars of the Heteromyinae were as far advanced as the corresponding teeth of some species of modern *Perognathus*, and were in practically the same state of evolution as was the permanent premolar of the same form, except for the greater development of the cingulum.

The evolutionary and paleogeographic problems suggested by the occurrence of these two species in Florida, so far removed from the present habitat of any member of the family, cannot be solved until considerable additional material shall have been collected. It is entirely futile to attempt to define the exact relationships of the different species, especially when they are represented by such fragmentary material, but there can be little doubt of the fundamental structural relationship between *P. magnus* and *Heteromys*, and that both of those forms, together with *Peridiomys*, *Diprionomys* and *Liomys*, can all be derived from an animal whose dental structure would be close to that of *P. floridanus*, as far as can be told at present.

[5a] Since this was written additional material has come to hand suggesting that the posterior cingulum may be primitive and is being lost in this form.

Proheteromys matthewi n. sp. (Fig. 96a.)

Holotype: A. M. N. H. No. 12896a.

Horizon and Locality: Upper Rosebud, 3 miles east of Porcupine Butte, South Dakota.

Diagnosis: P_4 quadrate, with heteromyine pattern clearly forecast; M_1 and P_4 both with no trace of posterior cingulum.

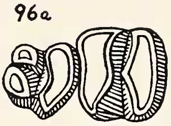


FIG. 96a. *Proheteromys matthewi*, holotype, A. M. N. H. no. 12896*a*, RP_4—M_1, × 10.

This species seems distinctly more primitive than any hitherto known member of the genus, having no peculiar features in its construction except the approximation of the anterior ends of the protoconid and mesoconid of P_4. This is one of the two specimens mentioned by Matthew (1907, p. 214) as being Rosebud relatives of *Heteromys*. The other and larger one is being referred elsewhere to the John Day geomyid, *Pleurolicus leptophrys*. These two specimens are the Miocene heteromyids mentioned in text books (see especially Osborn, 1910, p. 287 and Scott, 1913, p. 238).

Proheteromys parvus (Troxell), 1923

Synonymy:

DIPLOLOPHUS PARVUS Troxell, 1923.
HELISCOMYS PARVUS (Troxell), Hay, 1930.
MOOKOMYS PARVUS (Troxell), Wood, 1931.

Fig. 5; Troxell, 1923, figs. 3-5; Wood, 1931, figs. 1 and 3; Wood, 1933, fig. 5.

Holotype: Y. M. No. 10362, lower jaw with P_4—M_3, from Colorado.

Diagnosis: P_4 formed of four widely separated cusps, the anterior pair diverging toward the rear, so that further wear would form an anterior crescent with the concavity facing caudad; posterior cingula on P_4—M_2; M_3 bears a small hypostylid; very early stage in the development of the Y-pattern shown on metalophids of M_{1-3}; P_4 subtriangular.

The exact relationships of this species are still uncertain, but the characters as given above warrant its inclusion in this genus. The close approach of the protoconid and mesoconid of P_4 to each other would not necessarily be a primitive condition, but might merely be the initial stage in the development of a crescentic metalophid, seen to better advantage in *P. floridanus*. It is quite likely, however, that the triangular character of the tooth is due to recent enlargement of the mesoconid shown in its earliest state in *Heliscomys senex*, and that they have not yet moved far apart. The protoconids and protostylids of M_{1-3} are developing a sub-parallel trend, although it is definitely more primitive is this respect than is *P. magnus*. The significance of this tendency and of the pattern of the premolar, as well as of the posterior cingula, all of which show strong relationships with the Heteromyinae in general and *Proheteromys* in particular, was entirely overlooked by Wood (1931, 1932 and 1933). The hypostylid of M_3 is another suggestion of relationship to *Proheteromys* and *Peridiomys*. It is typically absent in *Perognathus* and *Heliscomys senex*, and hence, presumably, in *Mookomys*. M_{1-2} are much more quadrate in *P. parvus* than in *Mookomys* or *Perognathus*, where the anterior border is quite curved. In this again they approach *P. magnus* and *P. floridanus*, as well as *Heteromys* and *Liomys*, though to a lesser extent, and also show a much closer resemblance to the teeth of *H. vetus* than to those of the other species of *Heliscomys*.

It is unfortunate that the exact horizon and locality of this specimen are unknown. Troxell in his original description (1923, p. 157) says that both species of his genus *Diplolophus* are from the Oreodon Beds, Middle Oligocene. For *D. parvus*, he gives the locality (p. 158) as "probably Colorado." Mr. G. E. Lewis kindly looked up the original label in the Yale Peabody Museum, and informs me that it "states only that the specimen came from Colorado, and was found in strata presumably of middle Oligocene age. . . . The immediately preceding and succeeding numbers in the catalogue apply to unrelated localities" (letter, dated Jan. 29, 1934). The only other heteromyids that are of Oligocene age are the two specimens of *Heliscomys vetus* from the Cedar Creek Beds of Colorado, *H. senex* from the Brule of South Dakota, *H. gregoryi* from the Cook Ranch of Montana, and *H. hatcheri* of Nebraska, all Middle Oligocene. But *Proheteromys parvus* is much more specialized than any of these species, and also more so than the specimens of *Mookomys* discussed above, (pp. 89–90), from the Lower Miocene. It is comparable with the other species of *Proheteromys* from the Middle Miocene. This suggests the possibility that this specimen really came from the Middle Miocene. The Pawnee Creek Beds of Middle to Upper Miocene occur in the same part of Colorado as does the Cedar Creek Oligocene, immediately overlying it in some exposures. As the Pawnee Creek was known at the time Marsh's collecting in this region was done, as there is a considerable microfauna known from these beds, and as the original label apparently does not state the level with any certainty, it seems quite likely that this is the correct horizon for *P. parvus*, and it is so considered in the rest of this paper. Another possible source is the Lower Miocene Martin Canyon Formation, which also occurs in the same part of Colorado. But the close resemblance to the later species of *Proheteromys*, and the limited fauna known from the Martin Canyon, throw the balance of probability toward the Pawnee Creek. Of course, this problem can only be settled finally by the discovery of additional material of this species in beds of known age.

Peridiomys Matthew, 1924

Genotype: *P. rusticus*, Matthew, 1924.

Diagnosis: P_4 intermediate between those of *Proheteromys* and *Liomys*, showing initial stage of development of anteroconids; Y-pattern established, but lakes between the arms of the Y are ephemeral; H-pattern in lower molars; upper incisors smooth; masseteric crest gently sloping; jaw not unusually stout.

Range: Middle Miocene of Nebraska and Oregon.

This genus is represented by two species, *P. rusticus* and *P. oregonensis* (Gazin). It is very close both to *Proheteromys* and to *Diprionomys*, but is probably not ancestral to the latter, owing to the high development of the H-patterns. It is also distinguished from *Diprionomys* by the lesser development of the anteroconid of P_4; by the lack of sulci in the incisors; and, apparently, by the further development of the Y-pattern of the molars. Except for the well shown H-patterns, not represented elsewhere in this subfamily, this genus could be ancestral to all the later Heteromyines.

Peridiomys rusticus Matthew, 1924

Figs. 97-98 and Matthew, 1924, fig. 9.

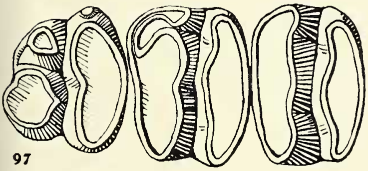
Holotype: A. M. N. H. No. 18894, from the Lower Snake Creek Beds of Sioux County, Nebraska.

Diagnosis: Anteroconid of P_4 closely united with protoconid; anterior cingulum by mesoconid; hypostylid developing on premolar; deep invagination between protostylid and protoconid of M_1; M_{1-2}

equal in size; M_3 not greatly reduced; H-pattern poorly developed; size large.

After cleaning shellac and matrix from the holotype, I can not doubt the correctness of Hall's belief (1930*b*) that this form is closely related to *Diprionomys*. It is, however, equally close to *Proheteromys*, but retains many characters distinguishing it from either, warranting its retention as a distinct genus.

The pattern of P_4 is quite different from that shown in Matthew's illustration (Matthew, 1924, fig. 9). Instead of clearly showing an X-pattern, with, in addition, lingual stylids, there is a typical heteromyine pattern of two lophs surrounding a central basin (fig. 97). There is no trace of the lingual stylids, though the matrix and shellac gave the impression that such were present. An anteroconid, not indicated in Matthew's figure, is clearly present, closely united to the protoconid. A short anterior cingulum extends from the mesoconid nearly to the anteroconid. M_1, when cleaned, clearly shows a valley between the protoconid and the protostylid, extending to the anterior side of the latter indicating a Y-pattern. This valley is quite shallow, as in *Liomys*, having been almost destroyed in M_1, and being entirely worn away in M_2. The molars show clear traces of the H-pattern, in the approximation of the protoconid and hypoconid, although they are not yet sufficiently worn to bring the pattern definitely into view. The large size of P_4 and M_3 (as may be told from its alveolus) is a typical Heteromyine character.



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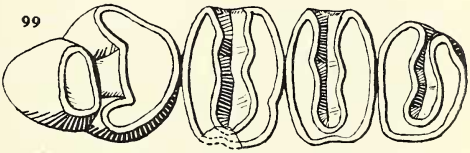

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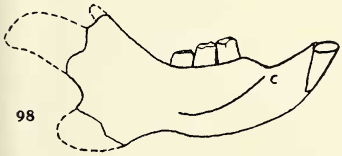

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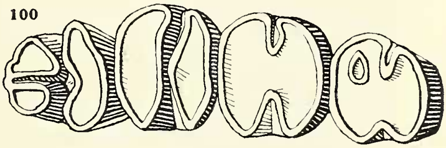

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FIG. 97. *Peridiomys rusticus*, holotype, A. M. N. H. no. 18894, RP_4—M_2, × 10.
FIG. 98. *P. rusticus*, A. M. N. H. no. 18894, lateral view, right lower jaw, × 2.
FIG. 99. *Periodomys oregonensis*, holotype, Cal. Tech., no. 371, LP^4—M^3, × 10.
FIG. 100. *P. oregonensis*, holotype, Cal. Tech., no. 371, RP_4—M_3, × 10.

The masseteric crest ends posterad of the mental foramen, as in Heteromyines, instead of above it, as in the other subfamilies. The massive character of the jaw noted by Matthew is due to incorrect restoration of the posterior part of the mandible, which appears more nearly to have been as shown in fig. 98. The posterior processes as shown by Matthew would differ fundamentally from the corresponding parts of all other heteromyid jaws. Moreover, broken surfaces show indubitably that parts have been broken off at the points shown in fig. 98. The size and shape of these have been restored from comparison with other heteromyids. In the portions of the jaw that are preserved, there is little difference in proportions from what occurs in other forms. The mandibular foramen is high on the ascending ramus, and there is no pit between M_3 and the base of the coronoid process.

Another jaw (A. M. N. H. No. 18895) from the same beds seems to belong to this species, although the cheek teeth are all missing. The size and proportions of the jaw, the position and shape of the mental foramen and masseteric crest, and the position of the mandibular foramen, are all the same in the two specimens.

Peridiomys oregonensis (Gazin), 1932

DIPRIONOMYS ? OREGONENSIS Gazin, 1932

Figs. 99-100; Gazin, 1932, Pl. 6, figs. 2, 2a, 3, 3a.

Diagnosis: Anteroconid just beginning to develop between mesoconid and protoconid of P_4; well developed H-pattern in lower molars; Y-pattern in M_3; heteromyine pattern of upper teeth clear, with first union of lophs on lingual, and next on buccal side; interorbital part of skull top much constricted; posterior lophs of $M\frac{3}{3}$ subequal to anterior lophs of same teeth; size medium.

Middle to Upper Miocene Skull Springs Beds of Oregon.

This species is essentially contemporary with the only other known member of the genus. Its teeth are slightly more brachydont than are those of *Diprionomys agrarius*, and less so than the earlier *Proheteromys*. The type species of *Diprionomys* consists merely of a lower jaw, but the pattern of its premolar is much nearer to that of *D. agrarius* than to that of *Peridiomys*, and further advanced than either. Gazin's doubtful reference of this species to *Diprionomys* was entirely justifiable, as this species was apparently closer to that genus than to any other then known.

The number of cusps in the protoloph of the premolar cannot be determined from any of the material available, as they have all been worn sufficiently to destroy all traces of the cusps. But the loph is quite broad, and is suggestive of a three-cusped loph. The entostyle has definitely established its union with the protoloph by moving forward. This forward movement has opened a valley between it and the hypocone, which gives an incipient J-pattern. The formation of this pattern (fig. 99) has not proceeded as far as in *P. magnus*, although the development of the protoloph and the heightening of the crown are much more advanced than in that species. The crest between the entostyle and the hypocone continues around to the posterior side of the latter, suggestive of the posterior cingula by which the enamel lake on the crown of *Heteromys* is surrounded. The lophs first unite between the protoloph and the entostyle, and next between the protoloph and the metacone, thus enclosing a central lake. M^{1-3} are similar to those of *Liomys* in their general appearance and in the absence of lakes in the crown of only slightly worn teeth. In unworn teeth of *Liomys*, however, lakes are present on the metalophs. No trace of such was to be seen in any specimen of *P. oregonensis*. The crowns are destroyed by wear progressively from rear to front. M^3 is not appreciably reduced.

P_4 shows great similarities to the corresponding tooth of *P. rusticus*, and approaches *Liomys* and *Diprionomys*. The protolophid is still essentially bicusped, but a small cuspule is in the process of formation on the side of the mesoconid, in the position of the anteroconid. As this cusp is united with the protoconid in *P. rusticus*, it is possible that it is an entirely different cusp being developed in this species, and that the distinction between the two species is greater than is apparent. The metalophid, also formed of two cusps, is longer than in *Proheteromys*. It shows no trace of the protostylid which occurs in *Peridiomys rusticus*. The premolar in *P. oregonensis* could have been derived from that of *Proheteromys floridanus* or *P. parvus* by increasing the length of the metalophid and by squeezing together the ends of the protolophid, accentuating the curve of that crest. The growth of the anteroconid, which is but faintly foreshadowed in this form, might tend secondarily to force the protoconid and mesoconid apart, resulting in the situation as seen in *D. agrarius* (see fig. 103). If this process were continued, the loph might become still straighter, as in *D. parvus*.

In the lower molars, the most striking feature is the fine development of the H-pattern. This interesting pattern has been acquired independently at least three times among the heteromyids—in *Peridiomys*, in *Dipodomys* and in *Perognathus*, and perhaps another independent time in *Microdipodops*. M_3 is not reduced. A pit is present in the metalophid of M_3, which seems to represent an enamel lake, derived from a Y-pattern, corresponding to the valley in M_1 of *P. rusticus*. Except for this one lake, no trace of such is to be found in the entire dentition. As wear normally affects the teeth from rear to front, it is remarkable that this should have been preserved in the third molar alone, especially as the first molar appears to have retained the lakes longest in *P. rusticus*. The presence of this type of lake, derived from the Y-pattern, is very characteristic of the Heteromyinae, although similar lakes occur in M_3 of *Dipodomys* and *Microdipodops*, but with a different origin.

As the top of the skull is destroyed, it is difficult to determine the boundaries of the skull bones. A natural brain cast is clearly shown (Gazin, 1932, pl. 6, figs. 2a, 3a). The bullae were not highly expanded and certainly did not meet ventrally. The top of the skull between the orbits is narrow, although the effect of narrowness is increased by the loss of the supraorbital portion of the cranium from the specimens.

It is unfortunate that this species, represented by such unusually fine skull material, should not be known from lower jaws with less worn teeth, to allow more complete comparison with related species. But *P. oregonensis* appears to foreshadow *Liomys* and *Diprionomys* in many characters of the dentition. It is definitely on a side-line as far as these are concerned, however, due to the development of the H-pattern in the lower molars. This species is nevertheless close to being ancestral to those genera. It is smaller than either *P. rusticus* or *D. agrarius*, the two most closely related species, as well as more primitive than either.

Diprionomys Kellogg, 1910

Genotype: D. parvus Kellogg 1910, from the Thousand Creek Beds of Nevada.

Diagnosis: Heteromyine type of P_4, consisting of two subequal lophs, uniting upon wear at their ends, and separated in the center of the tooth, thus surrounding what develops into an enamel lake; anteroconid large and distinct from other cusps; lophodont, but relatively short-crowned; no trace of additional lophs on P_4; no evidence of enamel lakes on the lophs of the molars; no H-pattern; upper incisors grooved; anterior part of masseteric ridge nearly horizontal; no depression between M_3 and the base of the coronoid process; locomotion subricochetal.

Lower Pliocene of Nebraska and Middle Pliocene of Nevada.

This genus represents a more primitive stage in dental evolution than do any of the recent members of the subfamily. As might be expected from their respective geologic horizons, it is considerably more advanced, in many respects, than the Middle Miocene *Proheteromys* from Florida, and appreciably more so than the Middle Miocene *Peridiomys*. The tendency to develop lakes on the lophs, by the double union of the protoconid and protostylid, in the lower molars, which is so characteristic of *Heteromys* and is already developed in *Proheteromys* and *Peridiomys*, is apparently entirely absent in *Diprionomys*. The fact that its upper incisors have developed sulci (in *D. agrarius*) would remove it, according to conservative views of evolutionary tendencies, from all possible ancestry to the living forms with smooth incisors. It is quite probable that this is the case, because of the divergent evolution of the limbs and skull, and hence this genus is indicated as a separate line on the phylogenetic chart (fig. 1).

Diprionomys parvus Kellogg, 1910

Fig. 101; Kellogg, 1910, figs. 17a, 17b; Hall, 1930*b*, figs. 9-10.

Holotype: Univ. Cal. Coll. Vert. Pal. No. 12566, right ramus of lower jaw with P_4—M_1, from the Thousand Creek Beds of Humboldt County, Nevada. Cotype, Univ. Cal. Coll. Vert. Pal. No. 12568, from the same locality.

Diagnosis: M_2 (judging from alveoli) wider than M_1; M_3 about half the size of M_2; protolophid and metalophid of P_4 about the same length, converging only slightly at the two ends; teeth fairly high crowned.

This species is known from two lower jaws, one of which has been lost. The teeth are badly worn. It is distinctly Heteromyine in aspect, however, due to the convergence of the two lophs of the premolar, surrounding a small, though clearly defined, central lake (fig. 101). As this species is the genotype, and as all of the species formerly referred to the genus, with the exception of *Peridiomys oregonensis* have Perognathine or Dipodomyine types of lower premolars, it has

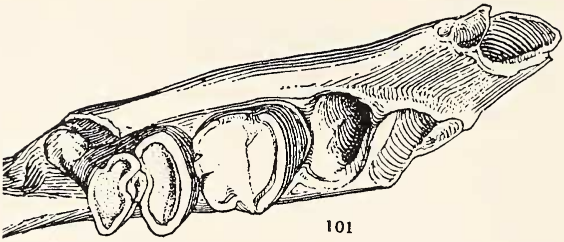

Fig. 101. *Diprionomys parvus*, After Hall, 1930*b*, RP_4—M_1, × 10.

been necessary to remove them to other genera. The great length of the protolophid of P_4 is remarkable, and places this definitely as the most specialized known member of a divergent line, developing from something similar to *D. agrarius*, and, more distantly, from the type represented by *Peridiomys*. The cutting edge of the lower incisor is broad and straight, suggesting *Heteromys*. The masseteric crest is nearly horizontal, as in typical Heteromyines.

This species is definitely more advanced than *D. agrarius* in the increased height of crown, more advanced lophization, and the increase in length of the protolophid of P_4, as well as its progressive straightening. The teeth appear to have considerably elongated roots, a point of resemblance to *Proheteromys magnus*, from Florida. While considering this species related to "*Diprionomys*" *tertius* and *Perognathus*, Hall (1930*b*, p. 302) nevertheless realized that there was a gap in the records here, saying that "*D. parvus* cannot stand as directly ancestral to *D. tertius* in the phylogenetic sense because the individual teeth differ too greatly in construction"—which is, if anything, an understatement.

Diprionomys agrarius n. sp.[6] (Figs. 102-128.)

Holotype: F. M. No. 14932, very complete skeleton, collected by Mr. J. H. Quinn, at Quinn Canyon, 13 miles north-northwest of Ainsworth, at the *Teleoceras* level, Lower Pliocene Devil's Gulch Beds.

Diagnosis: Auditory region apparently inflated, and ricochetal locomotion apparently fully acquired; size large; protolophid of P_4 curved as in *Proheteromys* and *Peridiomys;* M_1 wider than M_2; bones massive.

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[6] The specific name is given in honor of the Field Museum, which lent me this skeleton for study.

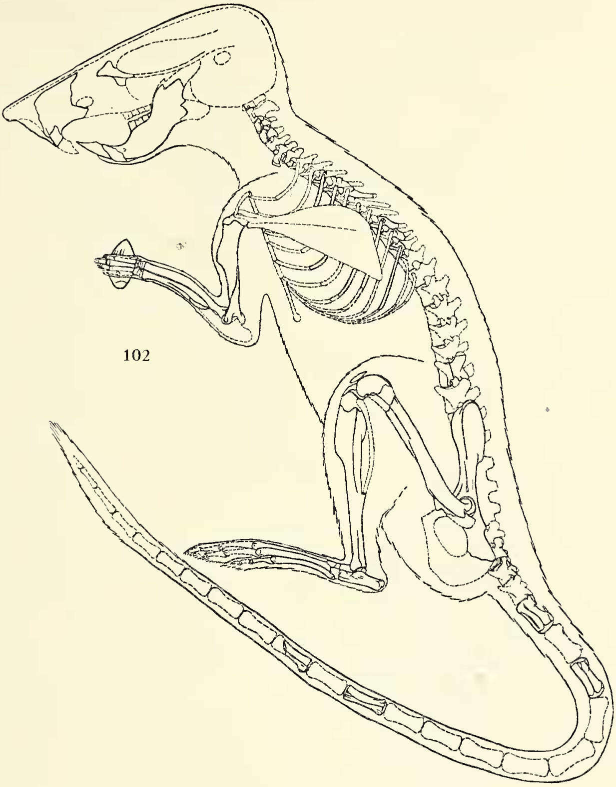

FIG. 102. *Diprionomys agrarius*, holotype, F. M. no. 14932, Restored Skeleton, × ⅔.

This species is represented by a good skeleton (fig. 102), though the skull is very fragmentary, and the upper cheek teeth are entirely unknown. The upper incisors are similar to those of *Heteromys*, except that there is a shallow groove slightly laterad of the center of the tooth (fig. 104). This groove is much more shallow than any other seen in heteromyids, except that occurring in the lower incisor of *Dipodomys spectabilis*. As in *Heteromys*, the lower cheek teeth are all of a similar size (fig. 103). M_1 is the widest, but only slightly wider than M_2. P_4 and M_3 are narrower than the others, although not by a great deal, and are of about equal width (see Table II). P_4 seems six-cusped: there are certainly three cusps in the protolophid, and probably

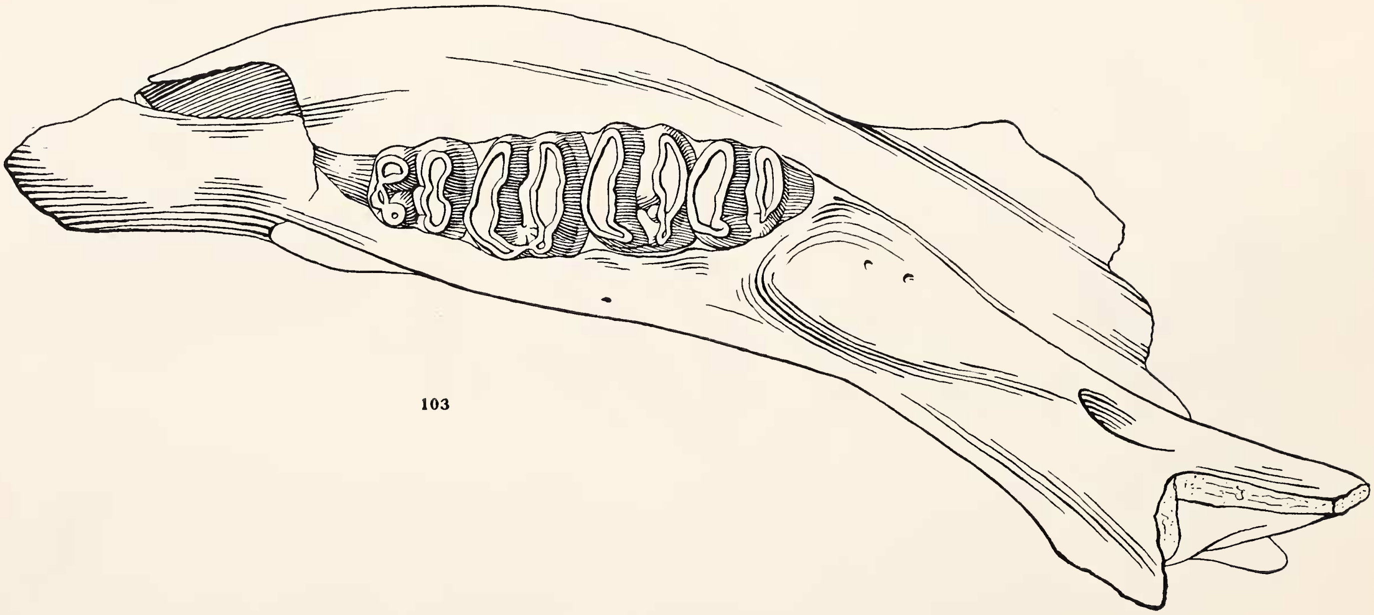

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Fig. 103. *D. agrarius*, F. M. no. 14932, Left lower jaw with P_4—M_3, × 10.

three in the metalophid, there apparently being a small hypostylid. The cusps in the protolophid are the protoconid and mesoconid, together with an anteroconid between and slightly anterior to them. The metaconid and hypoconid are clearly indicated. The hypostylid is already firmly united with the hypoconid. The metalophid is straight, while the protolophid is sharply crescentic, curving backwards at the two ends, which are thus approximated to the ends of the metalophid, showing considerable similarity to *Proheteromys floridanus* and to the two species of *Peridiomys*. The stylids of M_{1-3} are poorly developed in comparison to the other cusps. They seem but slightly differentiated from each other and from the cingulum, as, in M_1, they are already united, although the teeth are but slightly worn. The two lophs of M_1 are subequal and widely separated throughout, with no trace of the H-pattern. As a considerable portion of the uplands would have to be eroded before the bottom of the valley was reached, it is somewhat difficult to determine what the precise manner of union of the lophs would be. In M_2, however, it seems certain that, as in *Heteromys*, the next point of union would be between the lingual margins of the lophs. This tendency, however, is much less pronounced than in the living genera. M_3 has but a faint trace of a hypostylid, which is almost entirely fused with the hypoconid, but otherwise this tooth resembles the other molars. Wear affects the teeth progressively from rear to front.

The premolar of *D. agrarius* differs from that of *D. parvus* in that the protolophid is definitely U-shaped in the former, the two arms being directly sharply backward, whereas in the latter it is only slightly crescentic. This brings the lophs into much more certain contact at their extremities in the former species, and surrounds a much more clearly differentiated central basin. As is usual in the mid-Tertiary heteromyids, the cusps of the crowns of the teeth are much more clearly determinable than they are in the living members of the family. The lophs of the molars, as stated above, unite on the buccal side of the crown at a very early stage in the life of the animal. This is clearly the slightly modified ancestral cingulum. The narrowness of the cingulum is a point of close resemblance to the upper teeth of *Proheteromys magnus* from the Miocene of Florida. The minute size of the hypostylid of M_3 is decidedly reminiscent of the third lower molar in *Proheteromys parvus*, although there is no trace in *D. agrarius* of the posterior cingula found on the other three teeth of *P. parvus*.

The buccal half of the median valleys of the teeth of *D. agrarius* appears definitely to have been overdeepened, resulting in the union of the lophs upon wear between the metaconid and entoconid, whose sides extend out into the valley, forming a subsidiary dam. In both M_1 and M_2, the connection between the protostylid and hypostylid is almost as great as that between the latter and the hypoconid, giving the impression that the valleys open much more to the rear at the buccal side than is actually the case. In M_3, the lingual bar between the lophs is about as well developed as is the buccal bar.

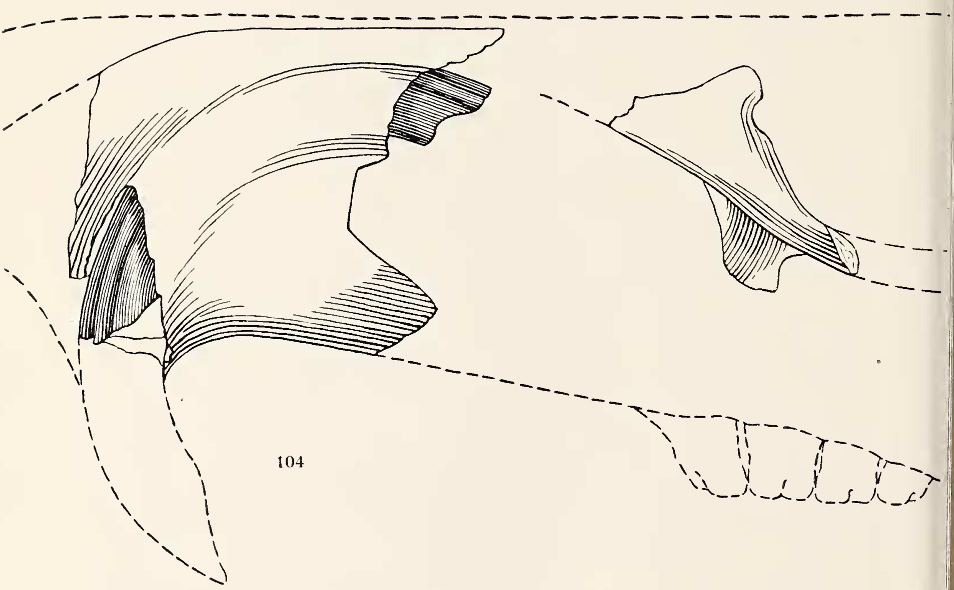

FIG. 104. *D. agrarius*, F. M. no. 14932, Anterior part of skull, × 5. Missing parts restored by comparison with *Heteromys.*

A few fragments of the skull are present, on the basis of which a restoration (figs. 102 and 104) has been made. Some of these are of an expectable type, while some are quite startling. The premaxillary is apparently quite close to that of *Heteromys*. There is no indication of any tendency toward a tubular type of nasals (which are not preserved), such as is found in *Dipodomys*. The zygomatic processes of both maxillae are present. They are about twice as wide anteroposteriorly as in *Heteromys*, indicating expansion paralleling *Cupidini-*

mus, although part of this is due to the larger size of this animal. There is a strongly marked crest along the antero-dorsal side of the zygomatic process, overhanging the masseteric fossa, which does not appear in *Heteromys*. The surface of articulation between the maxillary and the lacrymal is preserved, and indicates a lacrymal larger than in *Heteromys*. Some pieces which appear to be parietal or mastoid are present. The most remarkable, however, of all the fragments is the right occiput (fig. 105). This has a much stronger resemblance to that of *Dipodomys* than to that of any other heteromyid. The bone is highly compressed transversely, so that the lateral margins of the bone pass just laterad of the occipital condyle. The contact with the bones of the auditory region is clearly preserved on this lateral margin. This great compression can mean only one thing—that the auditory region had already become highly inflated, crowding the occipitals close together on the posterior margin of the skull. The whole of the occipital on the rear of the skull is compressed, which seems to mean that the inflation had been continued onto the dorsum of the skull as well. As in *Dipodomys*, the lateral margin of the occipital is everted, forming a much more sharply demarcated ridge than occurs in *Heteromys*. In this latter genus, the occipitals spread out over a large

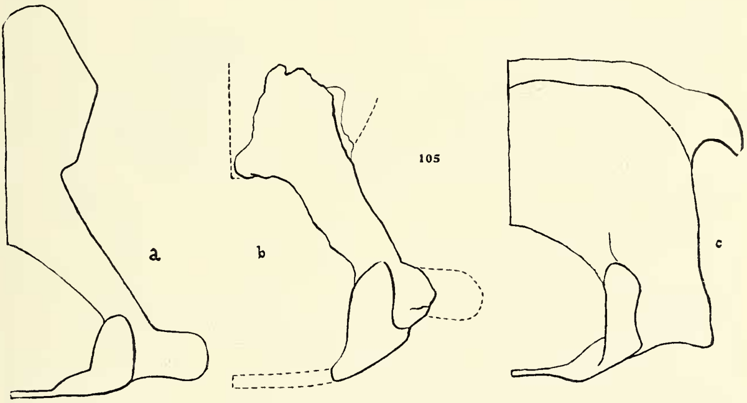

FIG. 105. Right occipitals, Rear view, × 5.
(a) *Dipodomys ordii*, A. M. N. H., D. C. A. no. 184.
(b) *Diprionomys agrarius*, F. M. no. 14932.
(c) *Heteromys longicaudus*, A. M. N. H. no. 3645.

portion of the occiput, and show no appreciable transverse compression.

The lower jaw (fig. 106) is little if any heavier than in *Heteromys* or *D. parvus*, the part preserved resembling what is known of *Peridiomys rusticus*. The masseteric crest is quite similar in all Heteromyines, being essentially horizontal, ending below the diastema, and not having a powerful knob at the anterior end. The anterior portion of the crest turns slightly upward, so as to avoid the mental foramen. In *Heteromys*, this last is circular, whereas in *D. agrarius*, it is oval, with its antero-posterior diameter about twice that of its dorso-ventral one. The coronoid is slightly higher than is that of *Heteromys*, and the condyloid process is of about the same proportionate size. The angle flares somewhat, and turns inward at its ventral margin, as in *Perognathus*, apparently indicating an inflated auditory region about the size of that in the pocket mouse. There is no pit between M3 and the base of the coronoid process either in *Heteromys* or *Diprionomys*, and the mandibular foramen in both forms is on the condyloid process, though it is distinctly more anterior in the latter form. The symphysis is broken off both jaws of this specimen, so that it is impossible to determine its exact limitations, but as the amount missing is not great, it seems safe to assume that it was short, essentially as in *Heteromys*.

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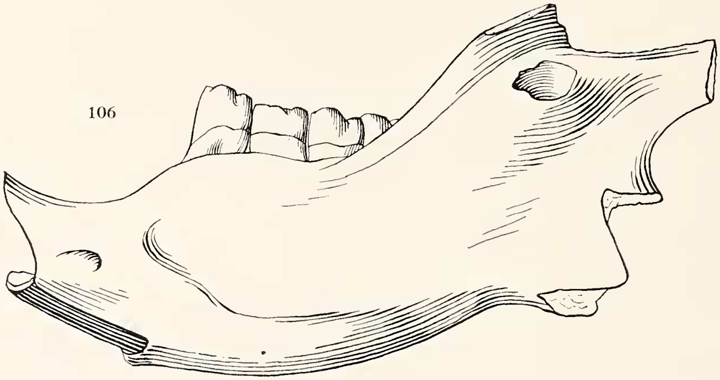


FIG. 106. *D. agrarius*, F. M. no. 14932, Left lower jaw, lateral view, × 5.

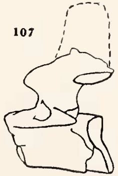
The right side of the atlas is present. The vertebrarterial foramen is present and quite large, whereas in *Heteromys* it seems entirely absent, its place being taken by a groove on the lateral margin of the transverse process, a distinctly specialized condition. The groove for the second cervical nerve, between the posterior articular facets of the atlas and the transverse process, is considerably deeper and more nearly covered over in *Heteromys* than in *Diprionomys*. The atlantal foramen is much larger than in *Heteromys*, and opens into the vertebrarterial canal. The transverse process is wider than in *Heteromys*, with a dorsal and a ventral segment distinctly separated.

The next vertebra present is the third cervical (fig. 107). On the ventral surface are two strong ridges converging anteriorly at the center of the rear end of the axis, and resembling the similar ridges on the ventral surface of the axis of *Heteromys*, which, however, do not appear on the third cervical of that form. They are even more closely similar to the ventral ridges occurring on the second to fifth cervicals of *Dipodomys*, which converge in a similar manner toward the rear end of the axis (Hatt, 1932, p. 692, fig. 24). The extension of these ridges onto post-axial vertebrae may be correlated with ricocheting and modification of the points of insertion of the M. longus colli which attaches to these processes. There is no indication of any fusion of this bone with the adjacent vertebrae, or of any other fusion of cervical vertebrae in this form, and enough bones are preserved to show that there could have been none.

The fourth cervical is also mostly preserved (fig. 108). There is no trace on the centrum of this bone of the diverging ridges described above, and the bone, except for the difference in size proportional to that between the two animals, seems indistinguishable from that of *Heteromys*.

The sixth cervical is well preserved (fig. 109). The post-zygopophyses are considerably reduced in their antero-posterior dimensions. An interesting character is a pair of short processes, one on either side of the neural arch, about half way between the spine and the prezygopophyses, which are quite well developed. No trace of these was observed in any other form, except for a slight roughness in *Heteromys*. The spine is higher than in *Heteromys*, which may be due merely to the larger size of the species. There are no ventral ridges. The ventral lamella of the transverse process is longer antero-posteriorly than in *Heteromys*.

Knobs are present on the dorsal surface of the neural arch of the seventh cervical, similar to those on the sixth (fig. 110), though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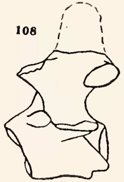
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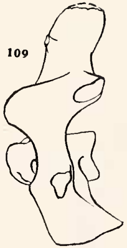
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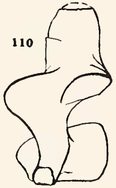
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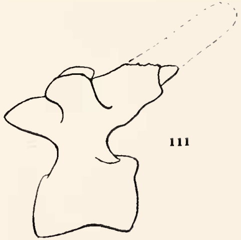
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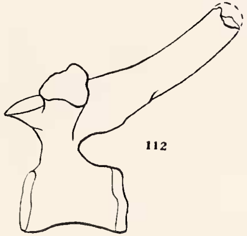
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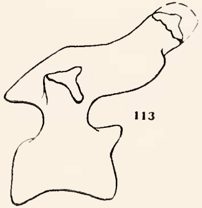
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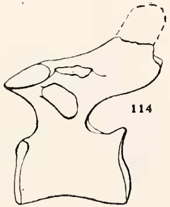
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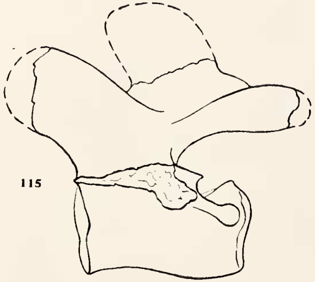
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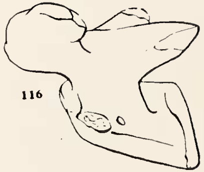
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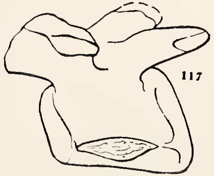
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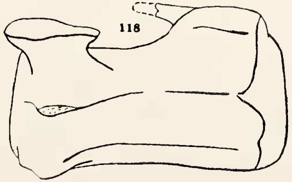
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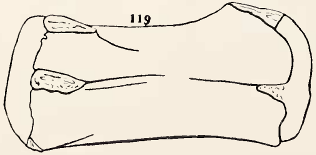
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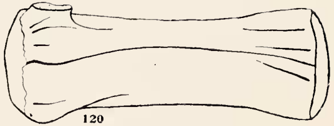
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For explanation of figures see page 187.

somewhat smaller. These knobs doubtless served for the attachment of some of the neck muscles, but what their modification was which caused the development of the processes, is uncertain. The neural arch is longer antero-posteriorly than in *Heteromys*. As in that genus, the transverse process is long and tubular, and is directed due laterad. A median ventral ridge occurs, better marked than in *Heteromys*.

The next vertebra preserved is the fourth thoracic (fig. 111). This bone differs from that in *Dipodomys* in the absence of notches on the posterior margin of the neural arch, to either side of the spine. In this respect, as in most others, it is close to *Heteromys*. The fifth thoracic (fig. 112) is similar to the fourth, but, as in *Heteromys*, it has a longer spine, thus differing from *Dipodomys*. In both of these vertebrae, the tubercular facets are high up on the sides of the neural arch.

The eighth thoracic (fig. 113) is similar to that of *Heteromys* and differs from that of *Dipodomys*. This is correlated with the decrease in the length of the thorax in *Dipodomys*, associated with its saltatorial habits, and due to the forward displacement of the center of motion of the vertebral column in that genus. The tubercular facet is moving down the transverse process toward the centrum. In the ninth thoracic (fig. 114), the facet is on the side of the neural arch, almost reaching the centrum. This again is a close parallel to *Heteromys* and a distinction from *Dipodomys*, in which the ninth vertebra

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EXPLANATION OF FIGURES

FIG. 107. *D. agrarius*, F. M. no. 14932, Third Cervical, left side, × 5.
FIG. 108. *D. agrarius*, F. M. no. 14932, Fourth Cervical, left side, × 5.
FIG. 109. *D. agrarius*, F. M. no. 14932, Sixth Cervical, left side, × 5.
FIG. 110. *D. agrarius*, F. M. no. 14932, Seventh Cervical, left side, × 5.
FIG. 111. *D. agrarius*, F. M. no. 14932, Fourth Thoracic, left side, × 5.
FIG. 112. *D. agrarius*, F. M. no. 14932, Fifth Thoracic, left side, × 5.
FIG. 113. *D. agrarius*, F. M. no. 14932, Eighth Thoracic, left side, × 5.
FIG. 114. *D. agrarius*, F. M. no. 14932, Ninth Thoracic, left side, × 5.
FIG. 115. *D. agrarius*, F. M. no. 14932, Fifth? Lumbar, left side, × 5.
FIG. 116. *D. agrarius*, F. M. no. 14932, Second Caudal, left side, × 5.
FIG. 117. *D. agrarius*, F. M. no. 14932, Third Caudal, left side, × 5.
FIG. 118. *D. agrarius*, F. M. no. 14932, Fifth? Caudal, left side, × 5.
FIG. 119. *D. agrarius*, F. M. no. 14932, Seventh? Caudal, left side, × 5.
FIG. 120. *D. agrarius*, F. M. no. 14932, Fourteenth? Caudal, left side, × 5.

is the anticlinal, whereas in *Heteromys* and *Diprionomys*, the spine, while becoming more erect, is still distinctly directed caudad. The centrum of another thoracic vertebra is present, which may be the tenth, partly because it is slightly longer than the ninth, and partly because the tubercular facet, which is barely separable from the centrum, suggests the tenth thoracic of *Heteromys*, in which it is the anticlinal vertebra.

One lumbar vertebra only is present, which is more suggestive of the fifth than of any other, in the heavy neural spine and relatively weak transverse processes (fig. 115). Moreover, there is a median ventral foramen, at about the middle of the inferior surface of the bone. A similar nutritive foramen occurs in the same place in the last three lumbar vertebrae of *Heteromys longicaudus*, *Dipodomys spectabilis*, *Dipodomys ordii luteolus* and *Dipodomys merriami*. The bone in *Diprionomys* cannot be either the sixth or the seventh lumbar, on account of the size and shape of the processes, and hence is probably the fifth. In *Dipodomys*, the median ventral foramen occurs in the last three lumbars, the last one or two pseudo-sacrals, and in the caudals. It is single except for the sixth lumbar, where it is paired. In *Heteromys*, the fifth lumbar has paired foramina, instead of the sixth. In L5? of *Diprionomys*, the foramen is single. Foramina may occur on the ventral surfaces of other vertebrae, but they do not have the large size and regular arrangement of the ones mentioned, which lie along the midline, and are of uniform size and shape throughout.

Two of the anterior caudals (figs. 116-117) are preserved. By comparison with *Heteromys*, they seem most similar to the first and second caudals. The resemblance is much more striking, however, to the second and third caudals of *Dipodomys spectabilis*, with which they are almost identical. They are thus assumed to be these bones. The neural arches are quite characteristic, the anterior end being much wider than the posterior. This is due to the lateral expansion of the mammillary process and of the rest of the zygopophysial region, which extends in a broad horizontal process as in *Dipodomys spectabilis*. This process is not present in any of the other forms compared. In *Diprionomys agrarius*, the process, instead of being parallel to the dorsal surface of the neural arch, slopes ventro-caudad at about 30°, being more nearly parallel to the ventral surface of the vertebra, which converges toward the dorsal surface of the neural arch, anteriorly. The lateral processes curve slightly more caudad at their posterior margins than in *Dipodomys spectabilis,* in which they are directed nearly at right angles to the antero-posterior diameter of the bone. The spine of what is here considered the second caudal is higher than that in the second of *Dipodomys,* and comparable to that in the first. The lateral surface of the bone is not hollowed out as a channel for the tendons and muscle fibers of the tail muscles, as it is in *Dipodomys,* where the neural arch and the transverse process extend some distance laterally, overhanging the passage. The transverse process is shorter than in *Dipodomys.* The ventral surface is less ridged in *Diprionomys,* though otherwise quite similar to that of *Dipodomys.* A small median ventral foramen is present toward the posterior side of the bone in both forms. The resemblance to *Dipodomys ordii* is definitely more remote than to *D. spectabilis,* which may indicate that the resemblances are size characters, since *D. spectabilis* and *Diprionomys agrarius* are very much of a size. In *Heteromys,* the lateral processes are absent, and there are quite large ventral ridges. In *Perognathus fallax,* the second caudal is quite similar to that of *Dipodomys,* though the lateral processes are much smaller than in *D. spectabilis* or *Diprionomys,* and there is not such an angle between the anterior and ventral surfaces of the centrum as there is in these two forms. In *Paramys delicatus,* the development of the lateral processes is in about the same stage as in *Perognathus,* but the transverse processes of the first few caudals differ from those of all the heteromyids in being directed caudad instead of cephalad.

The third caudal is similar to the third of *D. spectabilis.* The transverse processes are shorter than in that species and the spine is larger. The ventral surfaces of the bones are similar in the cephalad displacement of the median ventral foramina. The larger size of the spines of these vertebrae in the fossil suggests that the proximal portions of the tail were more fleshy than in any of the living heteromyids, while the similarity of the bones to those of *D. spectabilis* suggests a ricochetal habitus, the tail being used as in the kangaroo rats.

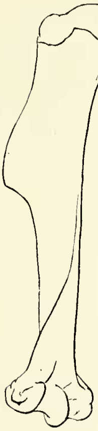
The next vertebra, which is tentatively called the fifth caudal, differs from all the bones with which it was compared, being intermediate in character between the fifth and sixth of *Dipodomys spectabilis, D. merriami, D. ordii, Perognathus fallax* and *Heteromys longicaudus,* (fig. 118). There is no trace of the strong median dorsal ridge found in *D. spectabilis.* The prezygopophyses are much further apart than in any of the bones with which this was compared, but do not show any trace of the lateral expansions of the first four caudals. The notch in the center of the transverse process is less abrupt than in *Dipodomys* or *Perognathus*. There are three ridges on the postero-ventral part, which run well forward, whereas, in *Dipodomys*, they are limited to the posterior portion of the centrum. The median ventral foramen is further forward than in *Dipodomys*, being placed as in *Heteromys*. Indeed, the entire ventral and dorsal surfaces of this bone resemble the latter genus, but the lateral aspects are quite different, the transverse processes in *Heteromys* being continuous for the whole length of the bone, with no trace of notching, and of uniform width. As the processes of the caudal vertebrae of *Microdipodops* are notched in the same manner as in *Diprionomys* and *Dipodomys*, it suggests very strongly that this is a ricochetal adaptation.

The next vertebra (fig. 119) is perhaps the seventh. The median ventral foramen is forward in the same position as in *Heteromys*, whereas in *Dipodomys* it is in the middle of the bone. The transverse processes are notched, differing from *Heteromys*, but the notch is a long, gentle curve, as in the fifth caudal, instead of being a sharp notch, as in the caudals of *Dipodomys*.

The fourteenth caudal seems to be the next preserved (fig. 120). It compares very favorably with the corresponding bone of *D. spectabilis*, and differs considerably from anything seen in *Heteromys*. The last vertebra is the anterior half of a bone which is very suggestive of the sixteenth caudal of *Dipodomys*.

In the tail, then, the curious combination of characters which occur in different sub-families is continued, with many resemblances to *Dipodomys* and *Perognathus* on the one hand, and equally striking ones to *Heteromys* on the other, indiscriminantly mixed. The former are probably habitus characters, due to *Diprionomys* having acquired a sub-ricochetal gait, while the latter seem indicative of fundamental relationships, as there is no similarity of habitus or locomotion which could have called them into being.

The head of the humerus is subglobular and essentially continuous with the shaft, as in *Heteromys* (fig. 121). The positions and sizes of the greater and lesser tuberosities and of the bicipital groove are about the same in the two forms, though the groove is somewhat deeper in *Diprionomys*. The epiphysis seems a little shorter in *Diprionomys* than in *Heteromys*. The deltoid processes of the two forms, are, however, quite contrasting. In *Heteromys*, it is a long, low ridge, sloping



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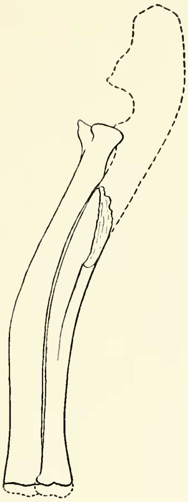

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Fig. 121. *D. agrarius*, F. M. no. 14932, Left humerus, lateral view. × 2.5.
Fig. 122. *D. agrarius*, F. M. no. 14932, Left radius and ulna, lateral side, × 2.5.

subequally both proximad and distad. In *Diprionomys*, however, it is very similar to that of *Dipodomys*, with a relatively gentle proximal slope, and a very steep distal one. The process is not quite as high at the distal end as in *Dipodomys*, nor is it thickened as much. As a result, the proximal slope is not as steep as in *Dipodomys*, being nearer *Heteromys* in this respect, while the distal slope is about 60°. The distal end of the bone is almost identical with that of *Dipodomys*, and, to a lesser extent, with those of *Perognathus* and *Cupidinimus*, with which the following comparisons could almost equally well be made. The supinator crest is large and flaring, instead of being slender and small as in *Heteromys*. The entepicondyle, as in *Dipodomys*, forms the most distal part of the bone, being extended some distance below the entepicondylar foramen, which is medial to the condyles as in *Dipodomys*, rather than proximal to them, as in *Heteromys*. The ulnar trochlea is somewhat distal to the radial, as in *Dipodomys*, rather than at the same level, as in *Heteromys*. There is no trace of fenestration of the supracondylar fossa, as there is in *Heteromys*. This bone has considerable resemblance to that of *Heteromys* in the proximal half, being more like this genus than like any other member of the family, whereas the distal half is entirely different, closely resembling that of *Dipodomys* and *Perognathus*. This is a striking combination of dissimilar characters, which is to be found throughout the entire skeleton of the animal. The humerus is quite massive. The respects in which the humerus approaches that of *Dipodomys*, however, are mostly concerned with characters which would be modified quickly by a change in the muscles, and hence would reflect the habitus of the animal. This gives another instance, if any such are needed, of the ease with which bones are moulded by muscles when the latter become modified in any manner.

The radius is remarkably short and thick, being about the same length as that of *Dipodomys ordii*, but almost twice the thickness (fig. 122). The whole bone takes part in the thickening, but the distal half shows it especially well. It is equally thickened when compared with *Heteromys*. The curvature is about the same in all three genera. The distal part of the ulna, which is all that is present in this specimen, is likewise thickened. On the postero-ventral surface of the ulna is a deep groove, not present in *Heteromys*, presumably serving as an origin for the flexors of the digits.

The thickening of the limb bones is extraordinary in an animal which, on other grounds, appears to be developing to a subricochetal stage, and is definitely greater than anything seen among recent heteromyids. Perhaps it is correlated with the (relatively) gigantic size of this species.

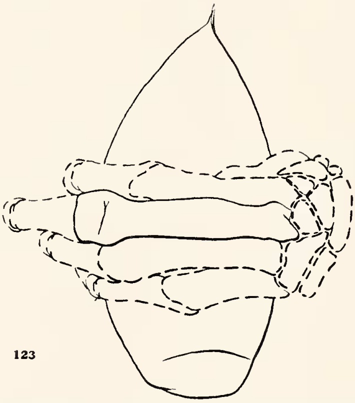

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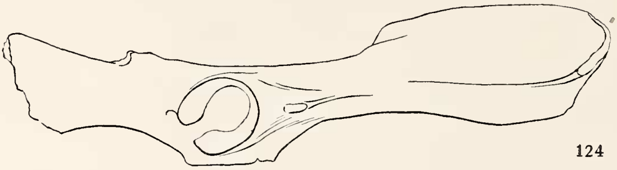
FIG. 123. *D. agrarius*, F. M. no. 14932, Left manus, × 5. Missing parts restored from *Heteromys*.

The only portion of the manus preserved is the third metacarpal, 15% longer than in *Heteromys* (Table III). The manus (fig. 123) is restored from that of *Heteromys.*

The entire right ilium, most of the right ischium, and considerable portions of the same bones of the left side are preserved (fig. 124). The iliac fossa of the ilium is much better developed than in *Heteromys.* The knob for the rectus muscle, anterior to the acetabulum, is similar in the two forms, and proportionately smaller than in *Dipodomys.* There is a deep notch in the dorsal border, marking the position of the posterior end of the sacro-iliac joint, which is much further forward in *Diprionomys* than it is in *Heteromys.* The sacro-iliac joint is 4.2 mm. high and 7.3 long, giving a ratio of 57.5, slightly higher than any found in *Heteromys* by Hatt (1932), appreciably higher than any he found in *Perognathus* and *Microdipodops*, and considerably higher than in *Dipodomys.* The extreme tip of the ilium is considerably everted, and the ventral half of the median surface is deeply grooved, anterior to the sacro-iliac joint, for the sacro-spinalis muscle. The medial wall of the acetabulum is very thin, but apparently was not fenestrated, although it is broken through in the specimen. Posteriorly, the acetabulum stands out more distinctly from the rest of the ischium than in *Heteromys.* The dorsal notch of this bone is in about the same position in the two forms, but is stronger in *Diprionomys.* The pubis appears to have been smaller proportionately in the fossil, though this is not certain, as the only thing to go on, in the absence of most of the bone, is the anterior tip, in and immediately ventral to the acetabulum.

Like the bones of the fore limb and of the pelvis, the femur is extremely thick and massive, apparently a characteristic of the bones of this species. The head (fig. 125), and greater and lesser trochanters seem quite similar to those of *Heteromys.* The third trochanter is slightly higher and slightly longer than in that genus. The shaft is quite straight, resembling that of *Cupidinimus*, but is not quite as straight as in *Heteromys*, the distal part being slightly curved. The third trochanter is nearer the proximal end of the bone than in *Heteromys*, apparently correlated with bipedal locomotion.

The tibiofibula, likewise, is heavier for its length than in any other heteromyid with which it has been compared (fig. 126), though it is closest to that of *Dipodomys spectabilis.* The cnemial crest does not become gradually reduced in elevation, but ends abruptly at its distal end, showing close similarity to *Perognathus* and *Dipodomys*, and in marked contrast to *Heteromys*. The median boundary of the posterior proximal fossa is marked by a strong, curving crest, only slightly represented in *Heteromys*, where the low crest uses up its



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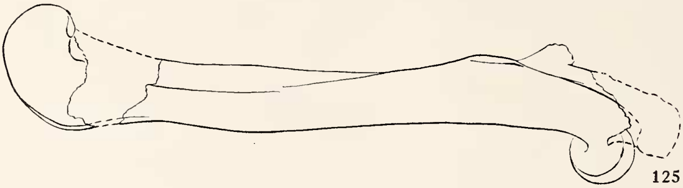

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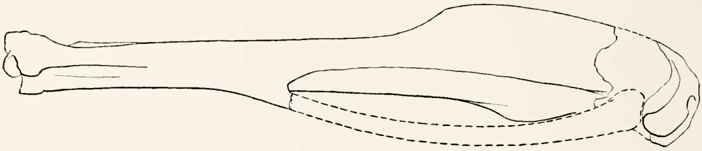

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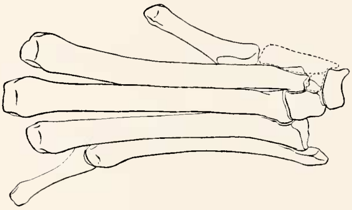

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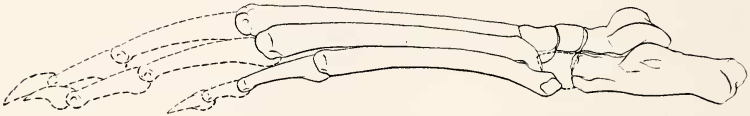

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FIG. 124. *D. agrarius*, F. M. no. 14932, Right ilium and ischium, lateral view, × 2.5.

FIG. 125. *D. agrarius*, F. M. no. 14932, Right femur, lateral view, × 2.5.

FIG. 126. *D. agrarius*, F. M. no. 14932, Left tibiofibula, lateral view, × 2.5.

FIG. 127. *D. agrarius*, F. M. no. 14932, Left pes, Dorsal view, × 2.5.
Composite of right and left sides of specimen.

FIG. 128. *D. agrarius*, F. M. no. 14932, Left pes, Lateral view, × 2.5.
Composite of right and left sides of animal. Missing parts restored from *Heteromys*.

energies in attaining considerable length, thus making the fossa much longer, and, at the same time, deeper, than in *Diprionomys*, where it is limited to the proximal quarter of the bone instead of to the proximal half. In the condition of both the fossa and its median bounding crest, *Diprionomys* is as nearly identical with *Perognathus*, *Microdipodops*, *Cupidinimus* and *Dipodomys* as it possibly could be. The medial malleolus is considerably longer than the lateral, as in *Cupidinimus*, instead of being nearly equal, as in *Perognathus* and *Dipodomys*, or absolutely equal, as in *Heteromys*. In all the limb bones, the points of most resemblance to *Dipodomys* are the size, shape and position of areas of muscle attachment, whereas the points of closest resemblance to *Heteromys* are the articular surfaces, general shape of the bones, and other factors not directly affected by changing muscles.

The pes resembles the other bones in being remarkably heavy (figs. 127-128). The neck of the astragalus is definitely wider than in *Heteromys*. The tibial trochlea of the astragalus is about the same length in relation to the fibular as in *Dipodomys*—that is, much shorter. In *Perognathus* and *Heteromys*, on the contrary, while the tibial keel is shorter, it is only slightly so. The neck of the astragalus of *Diprionomys* is about as in *Perognathus*, and wider than in *Dipodomys*. At its anterior end, the astragalus makes a contact with the cuboid, as in *Heteromys* and *Perognathus*, although it is not a large contact (see fig. 153). In *Dipodomys* and *Cupidinimus*, on the contrary, the contact is between the calcaneum and the navicular. There is little to note about the calcaneum. The navicular and ectocuneiform (the only other tarsals present in the fossil) appear to be essentially identical with the corresponding bones in *Heteromys*. The navicular is of essentially uniform antero-posterior diameter, as in *Dipodomys* and *Heteromys*, instead of tapering laterally as it does in *Perognathus*. The lateral margins of the cuneiform are essentially parallel to each other, instead of converging at the center to give the dorsal surface of the bone an hour-glass shape, as they do in the Dipodomyinae and Perognathinae. In this respect, the bone in *Diprionomys* resembles that in *Heteromys*.

The metatarsals, all of which are preserved on one side or the other, are much heavier than in *Heteromys*. The pollex is more reduced than in that genus, being essentially the same absolute size in the two forms, while there is a twenty-five percent difference in the dimensions of the other bones. *Diprionomys* is normal, however, in that metatarsal IV is shorter than III (also shorter than II), whereas in *Heteromys* and *Liomys*, as in *Microdipodops*, the fourth is the longest of all the bones in the pes. The metatarsals flare more, distally, than they do in *Heteromys*, approaching *Dipodomys* and being essentially identical with *Perognathus* and *Cupidinimus* in this respect. The shortening of the hallux is suggestive of saltatorial specialization, though by no means conclusive.

The skeleton of *Diprionomys agrarius*, when considered as a whole, presents a remarkable combination of characters found otherwise only in members of different subfamilies. The fundamental characters, however, which have been used above as subfamily characters, are all those of the Heteromyinae, with which group the genus is accordingly included. The characters of the lower premolar, and of the masseteric crest of the mandible, and the characters of the tarsus, would fit nowhere but in this subfamily. The many characters which are not met with elsewhere in the subfamily are parallels to ones found in *Dipodomys*, *Microdipodops* and *Perognathus*, and seem to represent modifications necessary in the acquisition of a ricochetal or sub-ricochetal habitus.

The revised intermembral index (see footnote 3, p. 103) is 42.3 and the intermembral index 61.1 (Table V). This gives a lower ratio than in *Cupidinimus* or any species of *Perognathus* measured, and is a close approach to the figures in *Microdipodops*, which is without any doubt a ricochetor. The bullae are greatly inflated, apparently being more so than in the essentially contemporary *Cupidinimus*. There are many resemblances of *D. agrarius* to *Microdipodops*, and, although nearly all of these are also shared with *Dipodomys*, there is a possibility that this form is an intermediate stage between *Microdipodops* and the Heteromyinae.

What little matrix was present with the specimen was fine sand grains resembling the deposits at Valentine. Barbour (1914) states that the Devil's Gulch consists of 225′ of unconsolidated sandy beds. The fauna as given by Barbour and by Barbour and Cook (1917) contains such forms as camels, oreodonts, numerous horses, proboscideans, dogs, and others, most of which are obviously plains dwellers, living in open country such as would be suitable for the development of saltatorial or sub-saltatorial rodents. The camels, oreodonts, and horses are certainly plains dwellers. Others, as *Teleoceras*, were subaquatic or frequenters of moist regions, and must have lived essentially in the locality in which they have been found. The amount of well-watered territory on either side of the Niobrara may have been no greater at that time than at present. The plains forms could then either have been washed into the river from the adjoining plains by heavy rains, or might have been entombed in quicksands or have died from other causes, when coming to the river for water.

?**Diprionomys** sp. nov. indet.

Two jaws (C. M. Nos. 10169 and 10180), collected by the author in the Valentine locality described above (fig. 34), in 1931 and 1932, represent what appears to be another species of *Diprionomys*. Unfortunately, all the teeth are missing from both of these jaws, which are the only complete or essentially complete jaws in a collection of a couple of dozen from this locality of which this is the case. There can be no doubt that both jaws represent a heteromyid. The masseteric crest is low, and nearly horizontal, ending anteriorly just above and behind the mental foramen, a character uniting them with *Diprionomys*. In No. 10180, there is a shallow pit beside M_3; in No. 10169, none is present. In both, the mandibular foramen is high on the coronoid process. This form is much smaller than *D. agrarius*, the alveolar length being 5.6 mm., which is, of course, also much larger than *Cupidinimus nebraskensis*, the only other heteromyid known from these beds (see Table II). The general shape of the jaw, of the angle, of the coronoid and condyloid processes, as well as the shape and configuration of the masseteric crest, all resemble *Diprionomys* more than they do any other heteromyid.

Hall (1930*a*, p. 315 and fig. 3) described and figured a tooth (U. Cal, Coll. Vert. Pal. No. 28542) from the Barstow Beds, which he called *Diprionomys* sp?. The general shape of the tooth as figured strongly suggests either one of the most advanced recent species of *Dipodomys* or else a Geomyid. The tooth is an elongate oval, with the enamel, in crown view, interrupted at both the buccal and lingual margins of the tooth. It is a high crowned, rootless form, as pointed out by Hall. It is much more advanced than are any known contemporary heteromyids, and compares fairly well with such late Tertiary and Pleistocene geomyids as have been described. It certainly is not referable to any known heteromyid genus other than *Dipodomys*, and should probably be called a Geomyid.

Liomys Merriam, 1902

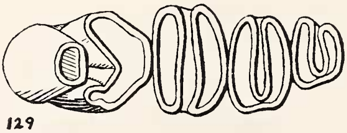
Figs. 129-132; Tullberg, 1899, Pl. 27, figs. 33-34; Goldman, 1911, Pl. 1, figs. 3, 3a and 3b.

Diagnosis: Cheek teeth medium crowned; upper incisors asulcate; only two lophs in M^3 and P_4; accessory lakes formed from Y-pattern short-lived; J-pattern in P^4 poorly developed; one or more anteroconids in protolophid of P_4; $M\frac{3}{3}$ slightly reduced; interparietal frequently paired; auditory region uninflated; locomotion scampering.

Range: Recent of Tropical and Sonoran zones from southern Texas and Sonora (Mexico) to Panama (fig. 157).

This genus carries slightly further the logical development of the tooth conditions in *Proheteromys*, *Peridiomys* and *Diprionomys*. The occlusal surfaces of $P\frac{4}{4}$ become much larger as the teeth become more worn, eventually attaining an area almost equal to that of all the molars, thus presenting an interesting partial parallel to the Mylagaulidae. The molars retain an approximately uniform size throughout life. This genus (Goldman, 1911, p. 9) "reaches its greatest abundance in semiarid, partially wooded regions, both plains and mountain slopes being well populated."

The anterior loph of P^4 appears always to be composed of three cusps, the central one the largest, and the two lateral ones compressed almost beyond recognition (fig. 129). The entostyle blocks the median valley, and forms the point of union of the two lophs. It is much more closely united with the rest of the metaloph than in *Heteromys*, where there is a deep re-entrant between the entostyle and the hypocone (see fig. 133), giving the median valley a Y-shape and the meta-



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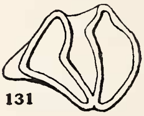

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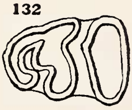

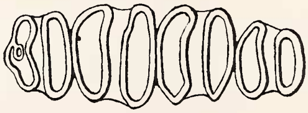

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FIG. 129. *Liomys vulcani*, A. M. N. H. no. 28366, LP^4—M^3, × 10.
FIG. 130. *Liomys vulcani*, A. M. N. H. no. 28366, RP_4—M_3, × 10.
FIG. 131. *Liomys irroratus texensis*, A. M. N. H. no. 3130, LdP^4, × 10.
FIG. 132. *L. i. texensis*, A. M. N. H. no. 3130, RdP_4, × 10.

loph that of a J. A posterior cingulum is present behind the hypocone, whose center sometimes unites with that cusp. More commonly, the union is at the two ends, surrounding a small pit, which soon becomes an enamel lake. Whether the two lateral cusps of the protoloph are the protostyle and paracone or protostyle and a buccal style, can not be determined without more Oligocene and Miocene Heteromyines, but it seems probable, by comparison with *Proheteromys magnus*, that both lateral cusps are styles, as the protoloph of that species is formed of the protocone and protostyle alone. The upper molars do not appear to develop the Y-pattern and its accessory lakes as readily as do the lower molars, and show nothing like the deep lakes found in *Heteromys*. Indeed, Goldman (1911, p. 32) states that in this genus, "loops of molar crowns normally without additional enamel islands even in young." However, in all specimens that I have seen which show very slightly worn teeth, such islands are present, though their life is very short. Goldman also states (op. cit., p. 33) that the *Liomys crispus* group differs from other members of the genus in that no lake is developed in the median valley of M^1. Such specimens of this species group in the American Museum collections as have teeth in the right stage of wear, however, do show a lake in the median valley of M^1 as well as of the other teeth. The third upper molar is but little reduced, but shows no evidence of the third loph to be found in some species of *Heteromys*.

In the lower premolar (fig. 130), a series of accessory cuspules have been developed in the position of the anteroconid, between the protoconid and the mesoconid, on the anterior margin of the tooth, varying from one as in *Diprionomys agrarius*, to several. There is frequently a direct connection between the protoconid and the mesoconid, in addition to one through the anterior cusps, so that a basin is developed in the protolophid, becoming a lake upon wear. There may or may not be a small posterior cingulum at the buccal margin of the metalophid, which, when present, brings about the development of the Y-pattern, so much more strikingly shown in *Heteromys*. This pattern is poorly developed in the lower molars, also, the anterior cingulum being extremely small. It is frequently at the center of the anterior margin of the tooth, instead of being at the buccal margin, so that the resultant lake will be in the center of the loph. M_3 is composed of six cusps, though the hypostylid is frequently extremely small.

When lakes are present in the lophs of the teeth of this genus, they are very ephemeral, being destroyed by wear with great rapidity, excepting the lake in the protolophid of P_4. The lakes which develop from the median valleys of the teeth, however, are of much longer duration.

The upper deciduous premolar is formed almost entirely of two crests, suggesting a two-cusped anterior and a three-cusped posterior one. A minute anterior cuspule is present, but is only slightly differentiated from the anterior slope of the protoloph, so that, upon wear, it forms an anterior extension of the protoloph, and never has an independent individuality of its own (see fig. 131). The two main lophs unite at their buccal margin, upon wear. There is thus a strong resemblance between dP^4 of *Liomys* and of *Dipodomys* or *Perognathus*, although the poor development of the anterior cuspule in the first genus suggests a separate line of evolution since early in the developmental history of the deciduous premolars, which is shown, on other grounds, actually to have been the case.

The lower milk premolar is composed of three lophs as is that of *Dipodomys* (fig. 132). The anterior one seems to be an elevated cingulum, not yet subdivided into cusps, which unites both buccally and lingually with the protolophid. The latter is a transverse row of three cusps, as is likewise the metalophid. The two anterior crests surround an enamel lake. This tooth is quite similar to dP_4 of *Dipodomys*, differing in the greater development of the cingulum of the two posterior lophs and its lesser development at the anterior end of the tooth. There is a very strong parallel to the pattern of the permanent premolar, in which the anteroconid is developing as an anterior crest, connecting the protoconid with the mesoconid. Fundamentally, however, the structure of the anterior part of the permanent and deciduous premolars is quite different, though they superficially resemble each other. The mesoconid of dP_4 shows the initial stage in the forward displacement characteristic of this tooth in *Dipodomys* and *Heteromys*.

This genus seems characteristically to have paired interparietals, 25 cases of all ages being observed in a total of 99 skulls studied, a ratio which suggests a simple Mendelian recessive. The zygoma is usually the widest part of the skull, although the diameter at the auditory meatus may be slightly greater. Ossicles are present at the antero-ventral lip of the meatus (Allen, 1904). The mastoid is, for a heteromyid, very slightly inflated. The bullae never reach the level of the grinding surface of the cheek teeth.

The skeleton is similar to that of *Heteromys.* The distal margin of the deltoid process makes an angle with the shaft of the humerus subequal to that of the proximal slope. The trochlea and capitulum are the most distal parts of the bone, extending distinctly beyond the end of the epicondyle. The percent of fusion of the tibia and fibula (see Table III) is very small—the smallest known in any heteromyid. As in *Heteromys*, the median border of the posterior fossa of the tibia is gently sloping instead of bearing a sharp hook. The astragalus and cuboid articulate, a long process of the latter extending between the calcaneum and the navicular. The tibial keel of the astragalus is only slightly shorter than the fibular, being 84% of its length. The navicular tapers in length toward both the medial and lateral margins. The ectocuneiform has nearly parallel sides. Slight rugosities are present on the dorsal surface of the sixth and seventh cervical vertebrae, as in *Diprionomys* and *Heteromys.* The ridges of the ventral surface of the cervicals are apparently limited to the axis. Median ventral foramina occur in the last five lumbar vertebrae. There are lateral expansions behind the zygopophyses of the third caudal vertebra similar to those in *Diprionomys*, though much smaller, but not present on any other vertebra.

Hall (1930*b*, pp. 203-204) considered that "*Diprionomys*" *quartus* and possibly "*D.*" *magnus* were closer to *Liomys* than to any other recent heteromyid. As I have endeavored to show, this does not now seem to be the case, those species being placed in different subfamilies, and the structural ancestry of *Liomys* being represented by such forms as *Proheteromys*, *Peridiomys* and *Diprionomys agrarius.*

Heteromys Desmarest, 1817

Synonymy:

SACCOMYS Fr. Cuvier, 1823.
DASYNOTUS Wagner, 1830.

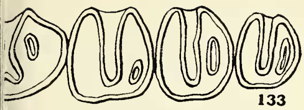
Figs. 133-144; Goldman, 1911, Pl. 1, figs. 1, 1a, 2, 2a.

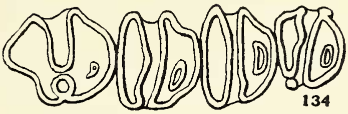
Diagnosis: Cheek teeth high crowned, with the most complicated pattern to be found in the Heteromyidae; anterior cingulum in lower and posterior cingulum in upper molars almost as high as the rest of the crown, giving, in early life, three lophs; upper premolar essentially as in *Liomys;* lower premolar with one or two additional anterior lophs not found in other heteromyids; auditory region uninflated; interparietal relatively narrow and never paired; locomotion scampering.

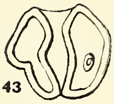
Range: Recent of tropical or subtropical portions of continental America from southern Mexico to Ecuador, and the Island of Trinidad.

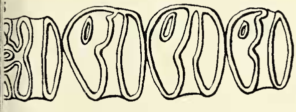
The cingula, which were shown in an early stage of development in the molars of *Liomys*, are much more progressive in this genus. They are essentially as high as are the main lophs, from which they are separated by deep valleys, whose depth is in part, at least, a function of the increasing height of the crown. In the upper teeth, the cingulum represents a migration of the internal cingulum along the posterior side of the tooth, breaking loose from the hypocone, following the course outlined above as occurring in *Proheteromys magnus*, and being the end stage so far attained in the development of the Y-pattern (figs. 133-134). The separation from the hypocone leaves a valley between that cusp and the cingulum, so that the metaloph assumes the shape of a Y. The growth of the cingulum on the posterior side of the tooth has caused a sharp bend in the metaloph, occurring at the point where the hypocone and metacone unite, increasing the similarity of the loph to a Y. This cingulum may extend only a small part of the way across the tooth, as in *H. australis*, where it extends only to the buccal margin of the hypocone. In *H. gaumeri* on the other hand, the cingulum reaches two-thirds of the way across the tooth, reaching the valley between the metacone and hypocone. There usually are no individual cusps detectable in these cingula, which are an outgrowth of the internal cingulum developed in the Oligocene and Miocene ancestors of the Heteromyinae. The lake in the metaloph is formed by the union of the lingual tips of the arms of the Y—that is, the lingual margins of the hypocone and entostyle. The metaloph of the third molar is composed of three cusps, although the entostyle is usually minute, and all three are closely compressed and firmly fused one to another. In the subgenus *Xylomys*, the posterior cingulum of M^3 is unusually large, being as well developed as either of the other two lophs. It unites at its center with the middle of the metaloph (Goldman, 1911, pl. 1, fig. 2).

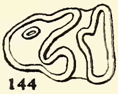
The lower molars are essentially mirror images of the uppers, the cingulum migrating from the buccal margin along the anterior side of the tooth, and the lakes are developed in the same manner. The third lower molar has a three-cusped hypolophid, although the hypostylid is small (figs. 135-136).

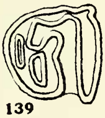












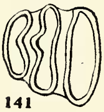


FIG. 133. *Heteromys crassirostris*, A. M. N. H. no. 37923, LP^4—M^3, × 10.
FIG. 134. *H. gaumeri*, A. M. N. H. no. 10458, LdP^4—M^3, × 10.
FIG. 135. *H. crassirostris*, A. M. N. H. no. 37923, RP_4—M_3, × 10.
FIG. 136. *H. gaumeri*, A. M. N. H. no. 10458, RdP_4—M_3, × 10.
FIG. 137. *H. fuscatus*, A. M. N. H. no. 28578, (lingual side at top), RP^4, × 10.
FIG. 138. *H. fuscatus*, A. M. N. H. no. 28578, RP_4, × 10.
FIG. 139. *H. fuscatus*, A. M. N. H. no. 28451, RP_4, × 10.
FIG. 140. *H. jesupi*, A. M. N. H. no. 15348, RP_4, × 10.
FIG. 141. *H. melanoleucus*, A. M. N. H. no. 14758, RP_4, × 10.
FIG. 142. *H. zonalis*, A. M. N. H. no. 36748, RP_4, × 10.
FIG. 143. *H. anomalus*, A. M. N. H. no. 4749, LdP^4, × 10.
FIG. 144. *H. anomalus*, A. M. N. H. no. 4749, RdP_4, × 10.

$\mathrm{P}\frac{4}{4}$ do not become extremely elongated with wear, as in *Liomys*, even though the teeth pitch strongly, the lower molars, especially, sloping forward at a sharp angle. The upper premolar is only slightly more specialized than that of *Liomys*. The protoloph is composed of three cusps, which are usually as closely united as are those of *Liomys*. In *H. fuscatus* (fig. 137), however, the three cusps are clearly distinguishable, and remain marked out from each other by grooves in the sides of the loph for a considerable length of time. The tooth of this species is the most complicated upper premolar studied, with numerous accessory crests and cuspules. The entostyle blocks the median valley as in *Liomys*, but is much more independent of the metaloph, forming a J of which the entostyle is the hook (fig. 133). In *H. fuscatus*, the free end of the entostyle often meets the center of the metaloph, uniting with the hypocone, so that an enamel lake is formed in this part of the crown. This, of course, is in addition to the lake formed by the elevation of the posterior cingulum at the posterior side of the metaloph.

The lower premolar, however, represents quite a high stage in specialization, reaching, in some species, a level higher than that of any other heteromyid tooth with which I am acquainted. In all forms, it is composed of at least three lophs, and in some of four (see figs. 135, 138-142). The metalophid, the most posterior of all the crests, is occasionally composed of but two cusps, the metaconid and hypoconid. In most species (as *H. fuscatus*, figs. 138-139), a third cusp is developing on the buccal margin of this loph as a minute stylid. In the more primitive species (as *H. jesupi*, fig. 140), the protolophid is composed of the protoconid, mesoconid, and an intermediate anteroconid, as in *Liomys*. Anterior to this is another crest, formed from an anterior cingulum. This cingulum unites with the buccal margin of the protolophid (as in *H. jesupi*, fig. 140), and makes its second union with the lingual margin of that loph, and appears to be formed of two cusps. These forms seem to represent the most primitive species of the genus that have come within the scope of this study. In these forms, a small crest is developing from the anterior side of the anteroconid, leading toward the cingulum, which it does not, however, reach until after considerable wear. Thus, in these species, a U-shaped loop is first formed, followed by a closed curve containing a single lake. In the next group of species, represented by *H. melanoleucus*, *H. lomitensis* and *H. anomalus* (fig. 141), the first point of union of the protolophid and cingulum is through this anterior spur of the anteroconid, after which the buccal and lingual junctions are made. In both of these groups, the cingulum either remains an undifferentiated ridge, or else is divided into an antero-lingual and an antero-buccal cusp. *H. australis* appears to be on the border-line between these two groups, sometimes one method of union being followed and sometimes the other, being like *H. melanoleucus* more often than not. In a third group of species, represented by *H. crassirostris*, *H. fuscatus* and *H. zonalis* (figs. 135, 138-139, 142), the anteroconid has been forced forward, apparently being squeezed out of the protolophid, forcing the cingulum to migrate in front of it. The anteroconid then forms the center of a fourth loph, with the rest of the crest being formed by a buccal and a lingual cingulum cusp, left behind by the migration of the anterior cingulum (fig. 135). In addition to these two cingulum cusps, the remaining part of the anterior cingulum is formed of two cusps in this group. In *H. crassirostris* (fig. 135), the anteroconid contains a small lake in its center, absent in all other species. It is possible that this lake indicates the fusion of two small cuspules such as are found in this position in some forms of *Liomys*, with a small pit left between them. Its absence in other species would then either indicate that the process of fusion has not been carried as far in *H. crassirostris* as in most species, or else that the other forms were derived from ancestors which did not have paired anteroconids. In *H. zonalis* (fig. 142), the migration of the anteroconid is in a transitional stage, the cusp having moved out of the protolophid, allowing the development of the mesostylid, and at the same time the anterior cingulum has been forced forward by the migration of the cusp, but as yet there does not appear to have been any tendency for increase in the number of anterior stylids, there still being but two, each of which unites upon wear with the anteroconid, so that a small lake is formed in front of this cusp.

The upper deciduous premolar is very similar to that of *Liomys* except that the protoloph is longer and more nearly equal in length to the metaloph (figs. 134, 143). It strongly resembles the permanent premolar, however, as in *Liomys*. It differs from the milk tooth of the latter form in the slightly greater reduction of the anterior cuspule, and in the development of an elevated posterior cingulum, giving rise to an enamel lake on the metaloph.

The lower deciduous premolar (figs. 136, 144) is fundamentally identical in pattern with that of *Liomys* and *Dipodomys*, having also essentially the same appearance as the permanent premolar of *H. zonalis*. In the species of *Heteromys* in which the deciduous premolar was observed, its characters were relatively constant, so that in the more advanced species, the permanent premolar becomes more specialized than the deciduous one, a result which is quite unusual among mammals. Not enough material was available to determine the range of variation in unworn milk teeth within the genus, but there appears to be a considerable amount. The median cusp of the protolophid has been squeezed out and pressed against the anterior cingulum, forcing it ahead of it. The number of cusps, if any are formed, in the anterior cingulum is indeterminable from any of the available material. Whether the migratory cusp represents a mesoconid as in *Dipodomys*, or an anteroconid as in the permanent premolars of *Heteromys*, is impossible to tell at present.

In tooth pattern, then, *Heteromys* represents the final stage to be met with among the heteromyids, having a much more highly complicated pattern than that of any other genus. Although the fossils which might be ancestral to this form are mostly unknown, the most important stages in the dental evolution can be determined with a fair degree of probability. In the middle Miocene *Proheteromys*, the initial stages can be seen. *P. magnus* shows two methods of developing enamel islands, both of which have been tried by later forms. It has incipient cingula on the posterior margin of the tooth identified as M_2, and a deep demarcation between the stylid and its associated cusp, which is almost ready, even in this species, to develop lakes. This is essentially the Y-pattern found in the molars of *Liomys* and *Heteromys*, although minute additional styles are present at the end of the lophs, in addition to the cingula, in the latter genus. The posterior cingulum of the lower molars of *P. magnus*, as that of *P. parvus*, was not destined to give rise to any permanent feature in the heteromyid teeth, and may indicate that these species represent a sterile side line. The next fossils are *Peridiomys* and *Diprionomys*, which show the premolar pattern of *Liomys* in its initial stage and fully developed, respectively. *Liomys* represents a stage intermediate between these forms and *Heteromys*, in which the Y-pattern has been fully acquired, and lakes are formed in the crown, but, due to the lack of hypsodonty, the lakes are very short-lived. In *Heteromys*, the increased height of crown makes the lakes deeper, and thus causes their life to be lengthened. As has been indicated above, the premolar of *Heteromys* is a development from the type that occurs in *Liomys*, but is certainly much more specialized. The *Liomys* type is only slightly more specialized than the tooth in *Diprionomys agrarius*. It is interesting to observe that the cingular cusps of the protolophid and metalophid of P_4 are just being acquired at the present time, which appears to be one of rapid evolutionary modification in all the members of this family.

In the skeleton, *Heteromys* is but slightly more specialized than is *Liomys*. The intermembral index (Table V) indicates quadrupedal locomotion. Both of these genera are closer to *Paramys* than are any other known members of the family, as far as the skeleton is concerned. The auditory regions of *Heteromys* are, if anything, less inflated than those of *Liomys*. The structure of the pes is relatively simple, and not widely removed from that of *Paramys*, the only peculiar feature being the increased length of metatarsal IV. The most striking specialization of the skeleton is the absence of the atlantal foramen in the atlas, its place being taken by a groove.

This genus at present ranges through southern Mexico and Central America, and into northern South America (see map, fig. 157). It occupies all areas from the semiarid, partially wooded mountains and plains of Mexico to humid, heavily forested regions, as in Ecuador, where the members of this genus live on slopes by water-courses (Tate, 1931).

The three main groups of structural characters available to paleontologists in making a classification of mammals are those of the teeth, the skull and the feet. If the evidence from all these sources points to the same arrangement of the genera, well and good. If not, one or more must be selected as of primary importance, and the rest relegated to a subordinate position. When all three indicate distinct arrangements, it is particularly unfortunate. In the case of heteromyids, skulls and feet are rare as fossils, even when compared with

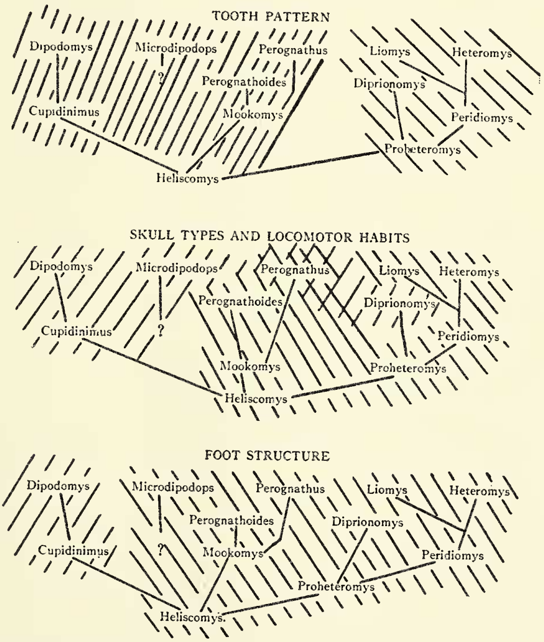


FIG. 145. Possible lines of subdivision of the Heteromyidae, on the basis of tooth patterns, skull types and locomotor habits, and structure of the tarsus.

the scanty collections of teeth. If all the major subdivisions were based on either skulls or teeth, essentially all of the fossils would have to be left incertae sedis. For this reason, as well as for the fact that tooth structure appears to me to be at least as significant as any other in this group, this has been made the primary point of division in the family. The three different possible divisions of the genera, using each of these three major criteria, are illustrated in fig. 145. Without a complete pedigree of all heteromyids, dating back to the Oligocene, it is, of course, impossible to determine the relationships with absolute and final certainty. It might have been better to have divided the genera in some other manner. But none at present appears any more satisfactory than that adopted here.

Having now considered the anatomy of the individual members of the family in some detail, it would be well to determine what general trends can be seen in the evolution of this group of rodents, and to organize the members of the family on the basis of such trends as are visible, after which the relationships of the family as a whole may be considered. Since the most important material available is the teeth, it will be worth while to review the main modifications which are found in these, before proceeding to the rest of the discussion.

The upper premolar, in the original members of this family, was probably a quadritubercular tooth, with protocone, metacone, hypocone and reduced paracone. This tendency for reduction of the paracone is clearly discernable in the earliest known upper dentition referable to the family, that of *Heliscomys gregoryi*, of the Middle Oligocene (fig. 146). By this time, however, an internal cusp had been added mediad of the hypocone, which is probably, by analogy with the molars, a derivative of a cingulum, although there is no direct evidence as to its homologies. By carrying this reduction of the paracone no further, the structure of the primitive Heteromyines could be reached, while but little further reduction would be needed to bring about the entire loss of this cusp, as in the Perognathinae and Dipodomyinae.

In the Perognathinae, the cusps of the metaloph unite to form a simple, curved loph, with its concavity facing forward, and the protocone unites with the metaloph, as the tooth is worn, near the center of the tooth—that is, with the hypocone or the space between the hypocone and metacone. In the Dipodomyinae, the point of union of the crests has moved buccally, paralleling the Perognathinae, but

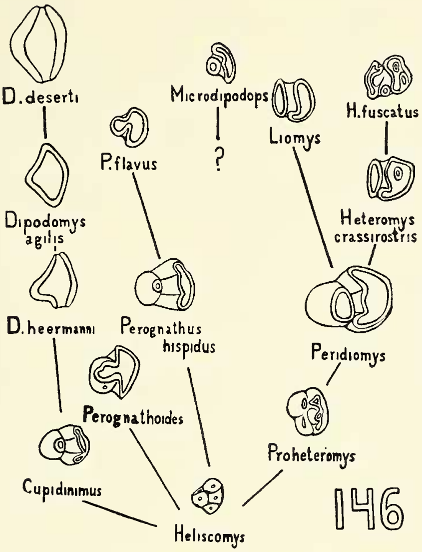


FIG. 146. Left upper premolars of heteromyids, all × 5.

differing in that the change in pattern is brought about by a forward movement of the metacone rather than by a lateral movement of the protocone, and further in that the protocone unites with the buccal margin of the metacone rather than with the space between it and the hypocone.

There seem to be two possible alternatives as to the origin of conditions now found in this tooth among the Heteromyinae. Which is correct cannot be determined at present, so the two alternative hypotheses are presented. Starting from a point similar to *Heliscomys gregoryi*, or even from a more primitive stage, in which the paracone was not so much reduced, the evolutionary tendency might have been to preserve and develop the paracone, as well as the protostyle. The result would be such a tooth as is found in the later Heteromyinae. The second alternative, which is more probable, intrinsically, is that the paracone has been lost in all the later heteromyids, and that a lateral style has subsequently been developed, similar to the lingual protostyle, in *Liomys* and *Heteromys*. In the earlier stages, supposedly ancestral to these genera, the protoloph consisted of two cusps, the protocone and protostyle, as is shown in *Proheteromys magnus* (fig. 93). This form is sufficiently close, structurally, to the later Heteromyines with a three-cusped protoloph to suggest that the cusp buccad of the protocone in those forms is a neomorph. The probability that this is the case is increased by the occurrence of such cusps in *Perognathoides*. There is so much parallelism among heteromyids as to suggest that if a pattern has been derived in a given manner in one form, the same pattern, if present in other forms, is very likely to have been derived in the same, or essentially the same, manner.

The parallelism between the permanent and deciduous premolars is so great in other respects that it seems reasonable to believe that they paralleled each other in this respect. *Perognathus* clearly shows that the third cusp of the protoloph of dP^4 is formed as an up-growth from a basal cingulum. In some unworn specimens of *Dipodomys*, there is a suggestion of three cusps in the protoloph of P^4, which, if correct, would seem, by comparison with *Cupidinimus*, likewise to be a recent modification. In unworn teeth of *Liomys* and *Heteromys*, there can be no doubt that three cusps are present. In these genera, the lophs first unite at the lingual margin of the tooth, between the protostyle and entostyle. A considerable valley is present between the hypocone and entostyle, in all Heteromyines, which varies in size with different genera, but is sufficiently large to prevent the progressive union of the lophs from lingual to buccal sides, making the loph J-shaped, so that after the protostyle and entostyle have joined, the next event is the union of the buccal extremities of the lophs, thus surrounding a central enamel lake.

The differences between the subfamilies in structure of the upper premolars appear to be quite fundamental, dating back at least to the Middle Miocene, and perhaps going back to *Heliscomys*. If it is necessary to include this last in any of the subfamilies, the structure of the upper premolar should place *Heliscomys gregoryi* among the Perognathinae.

The common ancestral form for the lower premolars of all the later heteromyids is such a tooth as is found in *Mookomys* or *Proheteromys*, of the Middle Miocene (fig. 147). The earliest known heteromyid, *Heliscomys vetus*, from the Middle Oligocene, has a premolar formed of but three cusps, the protoconid, hypoconid and metaconid. The next stage in the evolution of this tooth is shown in *H. senex*, in which a mesoconid is being formed at the antero-internal side of the tooth, from a cingulum, and a metaconulid is also present. The latter is

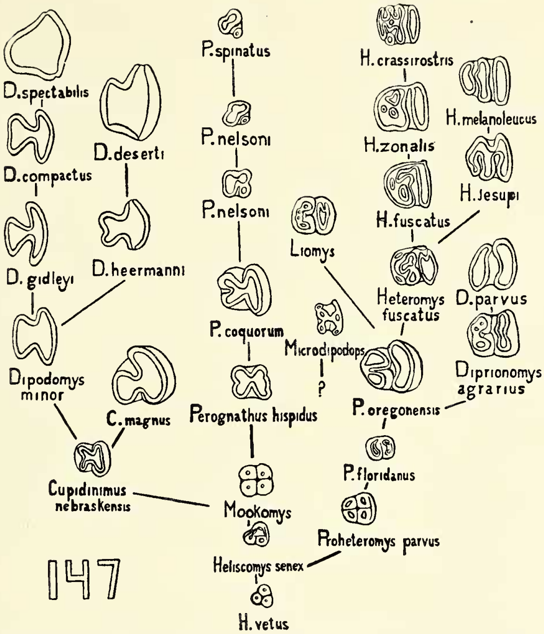


FIG. 147. Right lower premolars of heteromyids, all × 5.

probably aborted as the former grows in size. While it is possible that the metaconulid is retained and the mesoconid lost, the alternative seems more probable. This species is a welcome and long-sought intermediate between *H. vetus* and the Miocene members of the family such as *Mookomys* and *Proheteromys*, in which the tooth is subquadrate. In *P. parvus*, perhaps from the Middle Miocene, the two anterior cusps are closer together than are any other pair, suggesting the possibility that the anterior cusp of *H. vetus* simply divided in half to give the anterior half of the tooth of the later forms. This same pattern occasionally appears among living members of *Perognathus* (fig. 18). While this is a definite possibility, it can certainly not be taken as an established fact, and it seems more likely that the two cusps in *Proheteromys parvus* are approximated as the initial step in the formation of a crescentic loph such as is found in *P. floridanus*, especially as the anterior ends of the cusps are the closest together in the former species. While it is possible that the pattern in *Perognathus spinatus* is a reversion, it is considered more probably a case of degeneration.

In the Perognathinae, the protoconid and mesoconid normally remain much more distinct from each other than do the other two cusps, and, when they do unite to form a loph, they meet at an obtuse angle, with the concavity directed anterad. This tends to bring the two lophs into approximation, so that, as wear proceeds, the lophs unite in the center of the tooth, giving what has been called an X-pattern. Further wear merely enlarges this area of union, extending it both buccally and lingually. This type of premolar is found in *Mookomys*, *Perognathoides*, *Perognathus* and *Microdipodops*. In *Perognathus nelsoni* and *P. spinatus*, this tooth undergoes a series of mutations, developing a large number of different patterns, some of which approach or attain the patterns found in *Proheteromys* and *Heliscomys*, while others are unique. The ones that are like those of other heteromyids are probably caused by identical mutations of the same gene. This is an interesting addition to the group of cases showing that the greatest parallelism is between closely related forms, and indicates that the underlying causes of such parallelism are to be found not in similarity of environment alone, but also in similarity or identity of genetic composition.

The pattern of P_4 in the Dipodomyinae is similar to that in the Perognathinae, except for the progressive development of an extra cusp in the metalophid of the former. It is not certain at present whether this is a hypostylid or whether it is an intermediate cusp in the center of the loph, analogous to the intermediate cusps of the protolophid of the Heteromyinae, although the former is more likely.

In the Heteromyinae, on the contrary, the premolar follows the lead of the molars, and progressively develops numerous cingulum cusps, eventually reaching a much more complicated pattern than is approached by any of the molars. The earliest known Heteromyine, *Proheteromys*, shows no signs of cingulum cusps, the premolar being quadritubercular and differing from the corresponding tooth in the Perognathinae merely in having the protolophid convex anteriorly instead of concave. This convexity is due to the approximation of the anterior edges of the mesoconid and protoconid, instead of the approximation of their posterior margins.

The next stage is the development of an anteroconid between the mesoconid and the protoconid, just appearing in *Peridiomys rusticus* and *P. oregonensis*, and clearly shown in *Diprionomys agrarius*. *Liomys* indicates the next stage in one direction from this point, having the number of anteroconids increased, reaching as high as four in some specimens, though usually limited to two. The origin and manner of multiplication of these cusps is still uncertain, though it is probable that both can be explained under the general heading of budding from the base of the adjacent cusps. *Heteromys*, on the other hand, starting from a stage similar to that in *D. agrarius*, has developed cingula. These extend along the whole buccal and anterior faces of the tooth and part way around onto the lingual side. From them are developed the hypostylid, mesostylid and from two to four anterior cusps. It is possible that the anteroconids in *Liomys* represent derivatives from the cingulum, with the cingulum itself suppressed, but this is entirely hypothetical. In the more primitive species of *Heteromys*, but two anterior cingulum cusps are present, forming a loph anterior to the protolophid, thus giving a three-lophed tooth (fig. 147). In the progressive forms, however, the anteroconid or conids appear to have been squeezed out of the protolophid, and forced against the cingulum, carrying it forward ahead of it (or them). Two cingulum cusps now occur anterior to the anteroconid, and one on each side of it, forming, in this manner, a four-lophed tooth (fig. 135). What the mutual relations of the cusps in the four-cusped and two-cusped cingula are, cannot definitely be determined at present, though it is quite likely that each of the original two has split in half. By comparison with the deciduous teeth of *Dipodomys*, however (figs. 68-71 and 151), it would seem possible that the additional cusps represent separate swellings of the cingulum, tending to develop whenever the cingulum between two cusps became long enough to support a third cusp. A mesostylid develops in *Heteromys* after the forward migration of the anteroconid has left space in which it can form.

It may be seen, from this summary, that the evolution of the premolars gives the effect of an innate (or orthogenetic) tendency to develop cusps, which appear whenever there is space to allow their growth. Whether or not the presence of space is the causal character, this is certainly descriptive of the appearance of the manner of evolution, although the same results could be equally well explained as being due to the development of a new cusp, forcing the other parts of the tooth to move apart and make room for it. Here, as elsewhere in paleontology, it is difficult to distinguish between cause and effect, which explains the popularity of hypotheses involving orthogenesis.

The molars of all the later heteromyids are derivable from those of such a form as *Heliscomys*, through intermediate stages such as *Mookomys* or *Proheteromys* (see fig. 148). Originally the molars were doubtless quadritubercular, with a cingulum on the protomere. This early grew in elevation, and tended, in the first two molars, to become subdivided into two cusps. This is the situation in *Heliscomys*, the various species indicating successive stages in the growth of the cingulum. By the time the evolutionary stage of *Heliscomys gregoryi* had been attained, the protostyle and entostyle were of as great size as the protocone and hypocone, although the valley separating the two cingulum cusps was not as deep as the median valley in the other portions of the tooth. In the third upper molar of this stage, however, the cingulum was not subdivided, being formed of a single cusp, which may be considered the protostyle. The hypocone had not yet developed in this tooth, the internal cingulum continuing to the metacone.

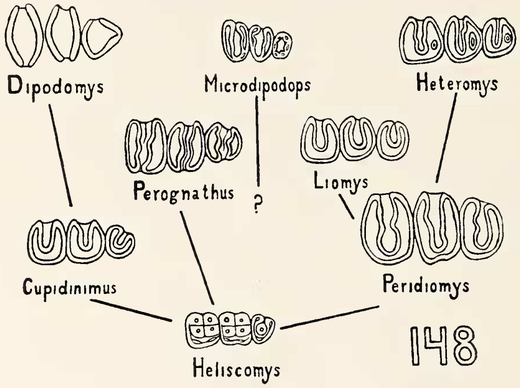


FIG. 148. Left upper molars of heteromyids, all × 5.

In *Mookomys* and later Perognathines and Dipodomyines, the six cusps of the first two molars unite to form lophs, which unite, on wear, at the lingual side—i.e., that originally bounded by the cingulum. In these forms, the union of the two lophs generally extends progressively from the lingual to the buccal side of the tooth. In two forms, *Perognathus penicillatus pricei* and *P. flavus mexicanus*, the lophs first unite via the protocone and hypocone, so that an H-pattern is developed, similar to that in the lower teeth. This has not been observed in any other forms. Sometimes, the flanks of the paracone and metacone extend into the median valley, so that a lake is formed on wear, though its life is very short. In *Microdipodops*, this is carried still further, and the buccal margins of the lophs in these two teeth curve toward each other, so that a central lake is soon formed. This lake has only a short life, because of the shortening of the occlusal part of the crown, but the situation appears to be closely similar to that in *Heteromys* and *Liomys*, where the lakes developed from the median valley have, however, a much longer life.

The Y-patterns described above as occurring in Heteromyines is developed when the entostyle separates from the hypocone and migrates along the posterior side of the tooth, forming a posterior cingulum, occasionally reaching as far as the metacone, while the hypocone becomes large, reaching the lingual margin of the tooth. This tends to increase the number of transverse blades in the tooth row, paralleling, on a small scale, the early stages in the Proboscidea. This has been a frequent evolutionary tendency among the rodents, almost every family having developed extra blades at least once. In most cases, the exact method of procedure is still uncertain, so it is interesting to observe that, in all members of the Heteromyidae in which extra crests are developed, they arise in whole or part as elevated cingula. It is this superficial parallel in the later and more specialized rodents which has induced some authors to postulate a real relationship between the Proboscidea and the Rodentia. A more detailed discussion of the latest of these (Friant, 1932*b*) may be found in Simpson (1933*a*).

The modifications undergone by M^3 are less certainly determinable. From the primitive stage as represented by *H. gregoryi*, with three main cusps and a single-cusped cingulum, the next stage appears to have been, in every case where data are available, a splitting of the cingulum to form two cusps, the posterior of which is called, for the sake of uniformity, the entostyle. If any additional cusps are developed, the usual procedure is for a bud to be given off from the buccal margin of the metacone, which becomes, in *Microdipodops*, sufficiently large to unite with the paracone as soon as the protostyle and entostyle have united, surrounding a large central crater. In *Dipodomys*, the union of the buccal cusps is accentuated, so that M^3 in this genus forms a U, opening linguad, the reverse of M^{1-2}. The situation in the living Heteromyines is less clear, and the problem is not settled by the fossils. In this group, the metaloph is three-cusped, the first point of union being lingual and the second buccal, as in M^{1-2} of the same forms, and as in *Microdipodops*. Whether the cusps are the same as those in the metaloph of *Dipodomys* and *Microdipodops*, or whether they are homologs of the cusps of the metaloph of M^{1-2}—i.e., whether there is a hypocone present—can not be decided at present.

In the heteromyids, as is often the case among rodents, the structure of the lower molars is nearly or quite a mirror image of the uppers, with essentially the same mode of evolutionary development. This is fortunate for the paleontologist, as it makes the interpretation simpler, one set of teeth helping to explain the other. Furthermore, as lower jaws of rodents are much more abundant as fossils than are uppers, it enables the phylogeny to be worked out with much greater certainty than if it were necessary to rely solely on upper teeth, as is essentially the case among Perissodactyls, for example. The course of evolution in the lower molars has not been identical with that of the uppers in all particulars, however.

The initial stage known for M_{1-2} was a four-cusped tooth, with a two-cusped external cingulum, the anterior cusp being much the larger. This is found in *Heliscomys vetus*. In *Paramys*, the lower molars are elongate antero-posteriorly. In *H. vetus*, they are square,

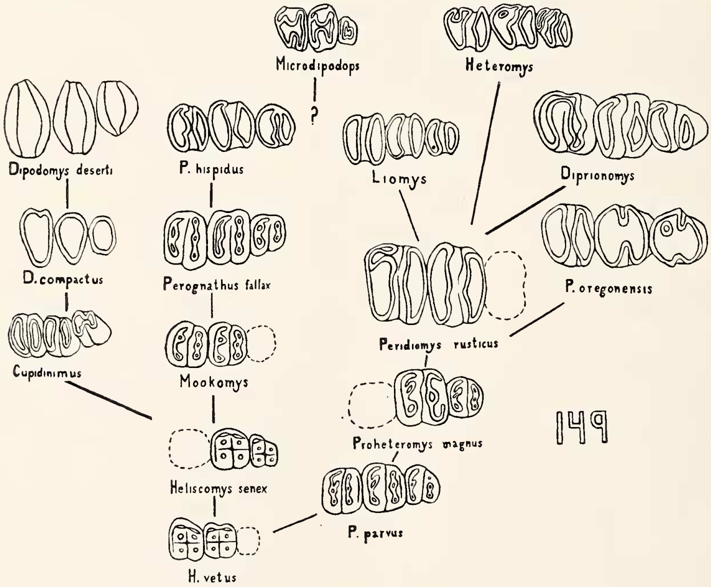


FIG. 149. Right lower molars of heteromyids, all × 5

but, disregarding the cingulum, the remaining part is much the same shape as in the corresponding teeth of *Paramys*. In *H. senex* and later members of the family, the teeth are elongate transversely, and the four primary cusps, homologous to those of *Paramys*, form a square. In the Miocene, the six cusps of the molars gave rise to two three-cusped transverse crests. Primitively, these crests united first at the buccal side, and continued to fuse progressively to the lingual side, as the tooth became worn. This is the case among most species of *Perognathus* at present, as well as among the largest number of fossil forms. In many forms, however, as in some species of *Perognathus*, and in *Dipodomys*, *Microdipodops* and *Peridiomys*, there is progressively a tendency for the point of initial union of the lophs to move toward the center of the tooth, so that the protoconid and hypoconid meet first, forming an H. In typical Heteromyines, the first union occurs at the lingual border, but the second is between the metaconid and entoconid, so that a central lake is formed, as in the upper teeth.

In M_3, there early appears to have been a divergence. In the earliest known form in which this tooth is preserved, *Heliscomys senex*, the hypolophid is two-cusped, the cingulum showing no signs of subdivision, though it extends the whole length of the tooth. In *Proheteromys parvus*, the hypolophid was three-cusped, consisting of an entoconid, hypoconid and minute hypostylid. This is essentially the basis for the pattern in later Heteromyines. In the other subfamilies, however, the more primitive members all appear to have a two-cusped hypolophid, the hypostylid apparently being absent, as in *H. senex*. This explains why, in some species of *Perognathus*, the two lophs unite lingually first, the metaconid being closer to the entoconid than the protostylid is to the hypoconid. In other species of *Perognathus*, as well as in *Dipodomys*, a small cuspule appears to be developing at the buccal end of the hypolophid, apparently being derived from the cingulum, as it unites shortly with the protostylid, making the pattern of this tooth agree with that of M_{1-2}.

In the later Heteromyinae, the lower molars develop accessory lophs in the same manner as do the uppers, the protostylid migrating along the front of the protoconid to form an anterior cingulum, while the protoconid moves out to the buccal margin of the tooth, making a Y-pattern.

One of the greatest specializations in cheek teeth, upper and lower, occurs in *Dipodomys*, and represents one of the most interesting parallels to the Geomyidae to be found among heteromyids. After the teeth have become entirely rootless and much compressed antero-posteriorly, the enamel becomes thin and finally disappears at the buccal and lingual margins of the tooth. This increases the efficiency of the scissors-like shearing of the enamel blades, by removing all superfluous enamel, since it would otherwise require an additional expenditure of energy to slide the lower teeth across the uppers, because, since the enamel protrudes beyond the dentine due to the more rapid erosion of the latter, it is only the enamel blades that actually come into contact with each other. The greater the area of enamel, the greater the friction in grinding. As the movement of the jaws is predominantly antero-posterior, the enamel at the buccal and lingual margins of the teeth has little or no functional value, and is hence eliminated, thus reducing the friction and increasing the efficiency of the shear. This is the stage that has been attained, not only in *Dipodomys*, but also in many geomyids, as *Geomys*, *Zygogeomys*, *Macrogeomys* and *Heterogeomys* (Merriam, 1895, pp. 96-97, where a fuller treatment of the mechanics is entered into). In the more progressive Geomyidae, as *Platygeomys* and *Cratogeomys* (Merriam, 1895, pp. 94-96), the process has been carried one step further, the enamel being reduced to a single strip, on one side of the tooth. As the blades are on opposite sides of the upper and lower teeth, and are concave in opposite directions, this represents a still further increase in efficiency, the food being caught between the concavities of approaching blades, and no enamel being present which does not come into use during every shear of the cheek teeth.

The evolution of the deciduous premolars is supported by much less paleontological evidence than is that of the permanent teeth. There is, however, a large amount of evidence available in the deciduous teeth of living heteromyids, which supplies almost all the structural intermediates between the more primitive permanent premolars (as those of *Proheteromys* and *Mookomys*), and the most specialized modern deciduous premolars. The two examples of milk teeth known among the fossils fit into this series in positions expectable from the general evolutionary stages of the animals in question. The most primitive known upper deciduous premolars differ from the permanent premolars of the same form in the possession of a cingulum running around the periphery of the teeth, connecting with all of the cusps. This occurs in *Proheteromys magnus* and *Perognathus apache*. The next

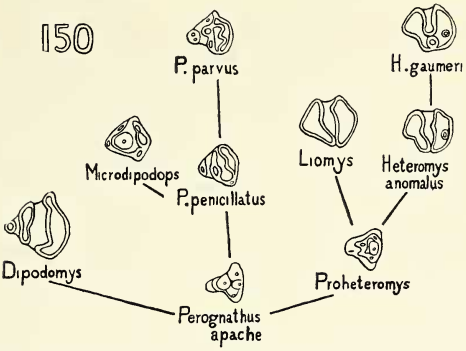


FIG. 150. Left upper deciduous premolars of heteromyids, all × 5.

stages, as shown in various species of *Perognathus*, involve the development of accessory cusps from the cingulum beside the protocone and in front of it. This results in the three-lophed tooth shown in the other modern genera. The variations from this type are but slight, the most pronounced being the occurrence of a lake in the posterior loph in *Heteromys*, suggesting the presence of a posterior cingulum, as in the permanent premolar.

In the lower deciduous premolars, the most primitive stage we know is again represented by *P. apache*. This tooth bears four main cusps, apparently homologous to those of the permanent premolar, an incipient posterior cingulum, and an anteroconid. The next stages involve strengthening this last cusp and the cingulum. Next, an

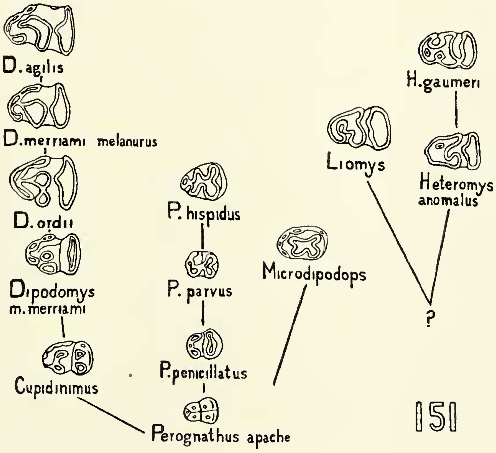


FIG. 151. Right lower deciduous premolars of heteromyids, all × 5.

anterior cingulum develops from the mesoconid to the protoconid, giving rise to two or more cusps. A migration of the anteroconid, as in P_4 of *Heteromys*, usually takes place, though it does not reach the extremes occurring in the permanent premolar. In *Dipodomys*, the cingulum does not reach the protoconid, ending at the anteroconid. Frequently, a buccal cingulum is also present, from which two or more stylids may develop.

It is worth noting that the deciduous teeth in *Dipodomys* and *Heteromys* are definitely less specialized than are the permanent premolars. In *Dipodomys*, the deciduous teeth are short-crowned, rooted, and do not develop enamel breaks. In *Heteromys*, they do not go to such extremes of specialization in the development of additional anterior lophs as do the permanent lower premolars. This is a reversal of the usual situation among mammals, the permanent premolars being more molariform than the milk teeth.

A further point of considerable interest is the comparative rates of evolutionary development of the deciduous teeth in different forms. In *Perognathus*, there is considerable modification of dP^4 while the lower tooth is relatively stable, whereas in *Microdipodops* and *Dipodomys*, the upper premolar stays essentially as it was in the more specialized types of *Perognathus*, and the lower premolar undergoes considerable modification, showing the lack of correlation between rates of evolution, not only for related structures in a given organism, but also for the same structure in related organisms. The fact that in *Heteromys* and *Liomys* there appears to be relatively little variation of the deciduous teeth, but a great deal in the permanent premolars, is another instance pointing to the same conclusion. Another instance of the same tendency toward lack of uniformity may be found in *Perognathus*, where the bullae of the subgenus *Perognathus* show much greater advances toward the conditions in *Dipodomys*, whereas the intermembral indices of the subgenus *Chaetodipus* are the more advanced. From these examples, it is clear that generalizations as to the rate of evolution, drawn from one structure in one line, would usually prove entirely incorrect if extended to another line, even if the two groups were closely related.

The great variation among the deciduous teeth of a single modern genus, as *Perognathus*, or in the permanent premolars of *Heteromys*, together with the considerable range of variation in other structures within a genus or even a species of modern heteromyids, suggests very definitely that the evolution of the family is proceeding at least as rapidly now as at any time in the past. Osborn (1934, p. 44) has cited the rodents as a group which have remained essentially unchanged since the Lower Pleistocene. From the apparent rapid evolution that the heteromyids are undergoing at present, as well as from the considerable structural gap occurring between such late Pliocene forms as *Dipodomys gidleyi* and the modern *D. ordii*, it would appear that among the Heteromyidae, at least, such is not the case. I believe the same to be true of other families of rodents. The apparent stability is probably due either to the absence of fossils, so that the variations cannot be discovered; to incorrect determination of the level in the Pleistocene from which fossil rodents were derived; to poor material, such as badly worn teeth; or to lack of familiarity with rodents on the part of the identifier. The small size of most rodents is doubtless a factor in this last item, at least. Benson (1933) has shown that marked differences have been acquired in *Perognathus*, of subspecific value, since late Pleistocene. In the southwest, races of pocket mice living on Pleistocene lava flows have developed striking differences in color from related forms living in adjacent sandy areas. Hinton (1926) has shown that in the Microtines, at least, there has been considerable dental evolution during the Pleistocene. In view of the great range among recent heteromyids, of the considerable gaps between the Pliocene and recent forms, and of the known modification of some forms since late Pleistocene, it would be extremely surprising if there were not essentially as much detectable variation among Pleistocene heteromyids as among an average family of Pleistocene Proboscidea, if the heteromyids were represented in collections by an equal amount of material.

In an interesting paper, Frechkop (1933) discusses the homologies of the cusps of mammalian teeth and the manner of their derivation. He has proposed the hypothesis of "homodynamie renversée," by which not only is the lingual side of the upper molars homologized with the buccal side of the lower, but also the anterior side of the uppers is homologized with the posterior side of the lowers. He cites much evidence of similarities between one end of the upper teeth and the other end of the corresponding lowers in support of this hypothesis, and considers (pp. 14-15) that *Heliscomys* is a clear instance in point. The patterns of the teeth of recent heteromyids, especially *Heteromys*, as described above, add additional material to his evidence.

There can be no doubt of the fact that, given quadritubercular teeth in both upper and lower jaws to start with, additional elements, among rodents in general and heteromyids in particular, are likely to be added at opposite margins of the upper and lower teeth—a cingulum or a series of cusps added at the anterior side of a lower tooth is likely to be balanced by a similar series at the posterior side of the corresponding upper tooth. If the tooth in question is in the center of the tooth row, such is almost certain to be the case. If, however, the tooth on which the additional elements occur is at either the anterior or posterior end of the tooth row, the effect in the other jaw is likely to be most pronounced at the other end of the tooth row. For example, in *Heteromys*, the three or four lophed P_4 is accompanied by a three lophed M^3, M^{1-2} being two or two and a half lophed; in *Microtus*, the two largest and most complicated teeth are M_1 and M^3; and in *Hydrochoerus*, the remarkably specialized M_3 is accompanied by a considerably complicated P^4. Other examples could be cited. This suggests, as a logical extension of Frechkop's hypothesis, that the most posterior tooth in the upper tooth row is homologous with the most anterior in the lower row.

But, even granting the apparent validity of "homodynamie renversée" when applied in a purely descriptive manner to accessory cingula and cusps acquired on the opposite ends of teeth in the upper and lower jaws, late in the evolutionary development, a serious stumbling block awaits the application of the hypothesis to the four primary cusps of such a form as *Heliscomys*. The four cusps in M^{1-2} appear without doubt to be paracone, metacone, protocone and hypocone, and in M_{1-2}, to be protoconid, hypoconid, metaconid and entoconid. These can readily be homologized with similar cusps in *Paramys*. In this latter genus, however, the upper molars also have a protoconule and a metaconule. No described form of *Paramys* shows any trace of a paraconid. But, by comparison with members of the Creodont-Condylarth-Insectivore stock of the Paleocene, to which *Paramys* is certainly related, there seems to be little doubt that a paraconid was present in the ancestors of *Paramys*, and that the entoconid grew up as the paraconid diminished, taking the functional place of the paraconid of the next tooth to the rear, and occluding with the valley between the protocone and hypocone. While this change in the cusps of the lower teeth was in progress, the cusps of the upper molar remained the same, except that the buccal styles of the Paleocene or Cretaceous ancestors are greatly reduced in *Paramys*. If the entoconid is a neomorph as suggested, to which cusp of the upper molar can it be homologous? According to this theory it would be equivalent to the paracone. But what was the homolog of the paracone before the reduction of the paraconid and the development of the entoconid? Apparently now it would be considered to be the metaconid. It seems obvious that the paracone cannot be homologous to the metaconid at one stage in the evolution of the tooth and to the entoconid at another, if these two cusps are different and if the paracone is the same cusp throughout.

Frechkop does not appear to realize the fundamental importance of the styles among the early mammals, as he considers them (p. 20) as forming, with the paracone and metacone, a single row of cusps of uniform origin, homologous to the internal row of the lower molars. The protocone, hypocone and conules cannot, however, be homologous to the trigonid of the lower molars, being later additions, developed as the buccal part of the upper molars was reduced, and as the function of the primitive teeth changed from shearing to partly grinding. If the various cusps that Frechkop is comparing have entirely different origins, it seems difficult to consider them homologous.

Another point that Frechkop stresses is the strong tendency for the development of three antero-posterior rows of cusps on the upper molars, after a primitive four-cusped stage has been attained. The heteromyids, which he cites as an example of this, cannot be considered as such, since the teeth consist of two *transverse* crests of three cusps each, with no indication of antero-posterior alignment, as can be seen in any partly worn teeth (see figs. 11, 13, 97, 103, etc.).[6a] In the Perissodactyls, a similar tendency for the formation of three rows of cusps, which Frechkop cites as occurring through the development of conules, would seem, if present at all, merely to be a retention of the conules, primitive structures lost in the ancestry of the Heteromyidae between *Paramys* and *Heliscomys*, as also occurs in many other rodents. I am not, however, familiar with any Perissodactyl which I should consider shows any tendency toward the acquisition of three

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[6a] Friant has stressed this supposed arrangement in three antero-posterior rows as a fundamental concept of her theory. As there is obviously no basis for this idea among the rodents, her theory may safely be disregarded at least as far as this order is concerned.

antero-posterior rows of cusps. There can be no doubt in the mind of anyone familiar with Cretaceous and early Tertiary mammals, that the conules are an ancient part of the teeth, although Frechkop (p. 20) considers them a secondary development in the Artiodactyls.

Therefore, it seems that Frechkop's hypothesis of "homodynamie renversée" cannot be accepted at its face value as an exposition of the homologies of the parts of mammalian teeth. Since it does represent some, at least, of what happens in the later evolution of rodent teeth, as is certainly the case in many forms (to the extent that a cingulum is developed at the anterior side of the lower molars at the same time that one is being formed at the posterior side of the uppers, as in *Heteromys*), it may be worth while to make an attempt at discovering the underlying cause. In movement of the jaws of rodents, there is a much larger antero-posterior component than in most mammals. This being the case, there would be a greater similarity between the stresses at the anterior end of the lower teeth and the posterior end of the upper teeth (or vice versa) than is usually the case. This would tend to allow similar developments of crests and cusps at the two ends, tending to be analogous, though not truly homologous, as they would not be derived from homologous sources. This process is well shown in *Heteromys*, and occasionally shows up in other heteromyids. The Geomyidae are an interesting case in point. Here the end stage of the reduction of the enamel of the molars is shown by *Platygeomys*, where the enamel is reduced to an anterior plate in the upper teeth and a posterior plate in the lowers. This seems to indicate analagous stresses rather than a homology of parts, as Merriam (1895) has indicated that the enamel retained is determined, not by the homologies of the part of the tooth it occupies, but by the mechanical principles necessary to give the maximum of efficiency to the shearing movements of the teeth. As the reduction, which thus appears not to be due to underlying homologies, affects the teeth in the same way as the increase, of parts, it seems best to refer them both to a common cause—analogous stresses in analogous parts of the teeth.

In spite of these objections to the hypothesis, it does present a useful aid in understanding the later development of rodent tooth patterns, provided that it is realized that the hypothesis merely describes the conditions as they occur, without explaining their origin. The later rodents do tend to develop a mirror imagery of such a sort that not only the outer side of the upper teeth resembles the inner side of the lowers, but also so that the anterior side of the uppers resembles the posterior side of the lowers, and the anterior tooth of the upper jaw tends in some cases to resemble the posterior tooth of the lower jaw. This tendency has not been stressed by most writers on dental evolution and mammalian paleontology, probably because insufficient work has been done on rodents to give a clear idea of their evolutionary tendencies. It is this tendency which forms the backbone of Frechkop's theory. As far as this is the case, we are in entire accord.

Among rodents, one very common variation is the development of a groove in the upper incisor, usually at about its center. The functional value of this, if there be any, is unknown, though Merriam (1895, p. 89) suggests that the division of the incisor into two sections enables the animal better to hold the food in place while cutting it with the lower incisors. Obviously, such a groove would increase the amount of enamel on a tooth of a given width, and so might be of use in forms that used their teeth in heavy gnawing. On the other hand, the presence of such a groove certainly would make the edge slightly less sharp, and so reduce the efficiency. Large forms such as the beaver and porcupine do not show any trace of sulci, though small grooves in large numbers cover the incisors of *Castoroides*, and strong sulci are present in both upper and lower incisors of *Hydrochoerus*. There may be little, if any, adaptational advantage in the possession of grooved incisors. It is very possible that there is a single gene which governs the grooving or absence of grooving in the incisors. Since this condition is so wide-spread among rodents, the possibilities for its development must likewise be wide-spread, so that the probabilities are that the mutation of a single gene is involved. Simple grooving certainly occurs too often to be a multiple-factor character, controlled by many genes. Complicated grooving, such as is found in *Castoroides*, might be the result of more complicated genetic modifications. The presence of grooves in the lower incisors of *Dipodomys spectabilis* and of supernumerary grooves in geomyids (Merriam, 1895, pp. 71-72) suggests the possibility that variations in depth and number of grooves might be due either to modifying genes or to a series of multiple allelomorphs.

In the Heteromyidae, we have a stock of nearly related rodents in which there have been several closely parallel evolutionary lines, as indicated by the structure of the cheek teeth and limbs. Within each of these lines, however, the incisors have been free to follow their own inclinations, and hence the two common types of incisors, grooved and smooth, have been developed, the former occurring independently at least three times, and the latter also at least three times, unless all of the smooth incisored forms are primitive survivals, as may or may not be the case.

If, as has been suggested, the incisor modification is the result of a single gene mutation, that is still no reason why the presence or absence of the groove should not be used as a diagnostic character of generic rank. If a complete evolutionary series were present in any group of organisms, the taxonomic separations would be entirely arbitrary, and the more nearly complete such a series becomes, the more arbitrary the splitting, from the point of view of "real" relationships. Any character is a "good" character if it can be used. Furthermore, if the grooves are caused by a single point-mutation, there is no conceivable reason (other than a teleological one) why the mutation, and hence the evolutionary modification, should not reverse its direction, so that we could have a smooth incisored form giving rise to one with grooved incisors, which might in turn give rise to one with smooth incisors. In this case, if the type of incisor were the only constant character separating two genera, Genus B might be descended from Genus A, and, a little later, Genus A might in turn be descended from Genus B. Fortunately, all of the genera discussed in this paper are based upon more than this one differentiating character. The presence of different types of incisors has not been considered, in this paper, as necessitating generic separation of two forms, if no other distinctions could be found in the available material.

Very little work has been done in the past on the teeth of heteromyids. The generic separations of the modern forms have been based largely on other characters. Coues, it is true, in establishing his subfamily Dipodomyinae, emphasized the rootless character of the cheek teeth as a distinction from the other groups. Goldman (1911) entered into the dental anatomy of *Heteromys* and *Liomys* in some detail. It is worth note that all the modern genera have dental distinctions of sufficient importance to warrant their retention as distinct genera even if they were known from nothing more than a single mandible. Furthermore, the relationships of the species as determined from cranial, skeletal and external characters are generally the same as those based on dental characters. The manner in which all of these different lines of evidence check considerably strengthens the case for the correctness of the results.

The primary skeletal modification occurring within this family is the development of the ricochetal type of locomotion. This has been acquired fully in three forms, *Microdipodops*, *Dipodomys* and *Diprionomys*. *Perognathus* and *Cupidinimus* represent initial stages in the same direction. No known Heteromyine other than *Diprionomys* has ever progressed beyond the scampering stage. The sub-ricochetal developments involve a proportionate increase in the length of the hind legs, until their functional length becomes about twice that of the fore legs, and, at the same time, an inflation of the auditory part of the skull, crowding upon the interparietal, parietals and occipital. The richochetal forms have increased the limb ratios until the hind leg is three times the length of the fore, and the auditory regions swell beyond all rime or reason. Correlated with the increase in ricochetal ability is a progressive fusion of the cervical vertebrae, increasing the stability of the head in the ricochet. As has been pointed out above (p. 143), it seems reasonable to believe that the limb modifications necessarily preceded the ricochetal development, whereas the fusion of vertebrae was a later modification making the animal better fitted for that type of locomotion.

The carpus shows distinct variations in pattern (fig. 152), which do not, however, seem to be sufficiently constant among the different groups of genera to be of value in supergeneric grouping. There appears to have been a progressive reduction of the centrale in the ricochetal forms, however. In *Microdipodops*, the trapezoid is the principal benefitor by this, reaching the scapholunar, as in *Heteromys*. In *Dipodomys*, on the other hand, it is the trapezium which enlarges, retaining its primitive contact with the centrale. In *Perognathus* and *Heteromys*, in which the centrale is not reduced, the pattern is much closer to that of *Paramys*, from which it differs, however, in the fusion of the scaphoid and lunar.

In the tarsus, there appears to be a much more important variation (fig. 153). In *Dipodomys* and *Cupidinimus*, the calcaneum has elongated until it makes a contact with the navicular, or even with the ectocuneiform. In all the other genera, the astragalus and calcaneum are of essentially the same length, but a process of the cuboid extends between the calcaneum and navicular, making a strong contact with the astragalus. Comparison with *Paramys* indicates that this is

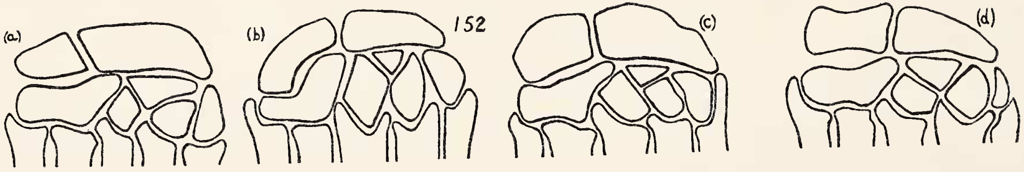

FIG. 152. Right carpus of modern heteromyids. Not to scale.

(a) *Perognathus fallax.* (b) *Microdipodops.* (c) *Dipodomys ordii.* (d) *Heteromys longicaudus.*

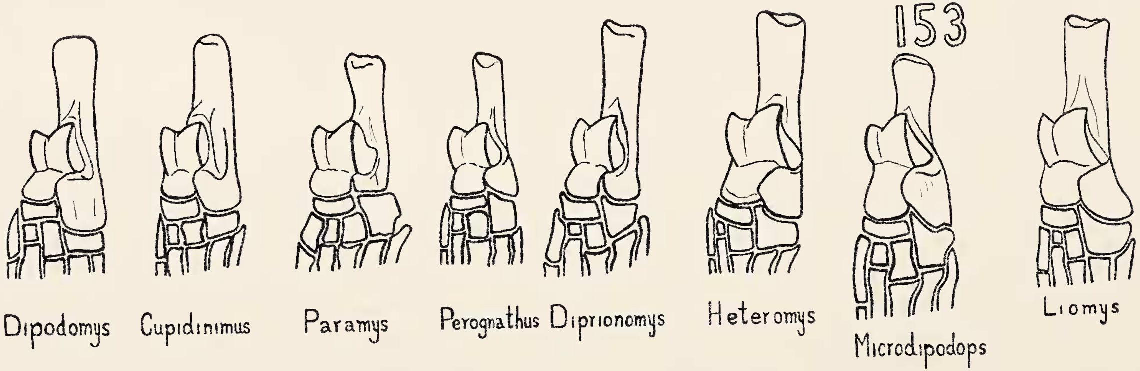

FIG. 153. Right tarsi of heteromyids. Not to scale.

perhaps a more primitive tarsus than that of *Dipodomys* and *Cupidinimus*, though it has been specialized in a different direction.

In studying the evolution of any group of animals, it is very important to know which is the most primitive, so that the direction in which the evolution is proceeding and the manner in which it does so may be determined. If a mistake is made at the beginning in selecting the wrong type as the primitive one, the results will be fantastic. It appears to have been an erroneous initial assumption of this sort which has led to the remarkable conclusions reached by Friant (1932*b*) and Schreuder (1933), who consider the "Hystricomorphs" the most primitive rodents, intermediate between the Multituberculates and the other rodents, and all rodent evolution to have been progressive simplification and degeneration. As Simpson (1933*a*) has shown and as Frechkop (1933) has indicated, all the paleontological and other evidence points to the Multituberculates being an entirely independent group from the placental mammals. One unfortunate feature for the Multituberculate hypothesis is that the rodents which show the supposed relationship most clearly are the later members of the order, the Eocene forms *all* having quite simple, primitive teeth, and the teeth of the earliest known rodents are more dissimilar to those of Multituberculates than are the teeth of most living rodents. As Simpson (1933*a*) has discussed Friant's hypothesis at considerable length, it does not seem necessary to repeat his arguments, with which I am in full agreement. It may be worth while remarking, however, that, although Friant has shown (1932*a*) that jaw movements do occur in embryo rodents, resulting in the destruction of the enamel caps of the cusps of caviids before birth, it does not seem entirely clear how such jaw movements could affect the germs of teeth before the teeth were erupted, nor how they could bring about changes in the tooth pattern after eruption.

In an effort to avoid such errors in initial assumptions as much as possible, no member of the family has been selected as having the most primitive skeleton, with which to compare the others. When a primitive form was desired, the skeleton of *Paramys* was used. If *Paramys* should prove not to be a primitive rodent, but one of the most specialized, as would be a necessary conclusion from Friant and Schreuder's points of view, there would then be no possible method of distinguishing a primitive from a specialized form, except in accordance with some preconceived opinion. The skeleton of *Heliscomys* would undoubtedly be more primitive than that of any other member of the Heteromyidae, but unfortunately it is yet to be collected. Most mammalogists would agree that the skeletons of *Liomys* and *Heteromys* are more primitive than those of *Perognathus*, *Microdipodops* and *Dipodomys*. This is without doubt the case in respect to those characters which are the most noticeable in the latter group—i.e., those points in which they are specialized. With respect to the structure of the metatarsals, it appears extremely probable that the elongation of metatarsal four is a specialization in *Liomys* and *Heteromys* carrying them beyond *Perognathus* and *Dipodomys*. If *Paramys* be the primitive type, does the distal migration of the third trochanter in *Heteromys* remove that form further from *Paramys* than the equal proximal migration of the third trochanter in *Dipodomys?* As far as the sum total of known skeletal characters goes, *Liomys* is probably the most primitive member of the family, with *Heteromys* second, although there are many features in the manus and pes of *Cupidinimus* which make it more closely united to *Paramys* than is any other heteromyid. But in cheek tooth characters, both *Heteromys* and *Liomys* are much more specialized than is *Perognathus*.

Fossil heteromyids are still sufficiently rare so as to make correlation by means of them alone uncertain, but definite advances have been made in this direction, as is shown in the chart (fig. 1). *Heliscomys* is known only from the Middle Oligocene; *Proheteromys* only from the Middle Miocene; *Diprionomys* only from the lower part of the Pliocene; *Liomys* and *Heteromys* are unknown in the Tertiary; *Mookomys* and *Peridiomys* are Miocene; *Perognathoides* is Upper Miocene and Lower Pliocene; *Cupidinimus* is Pliocene; *Dipodomys* ranges from the uppermost Pliocene to recent; *Microdipodops* is unknown as a fossil; and *Perognathus* has the longest range of all, extending from the Upper Miocene to the present. While this is not sufficient to allow exact and detailed correlations, it is at least a start in the right direction, and gives a foundation upon which additions can readily be built.

It is generally considered that the Miocene represents the initiation of the high plains character of the western part of the United States, with the development of the grasses as the dominant plains flora. This was the time when the Equidae and various Artiodactyls developed a grazing type of dentition. The development of the plains facies was correlated with increasing aridity, due to the elevation of the mountains to the west, cutting off the moisture which had supplied the forests of the Eocene and the well watered plains of the Oligocene. As Hatt (1932, p. 626) points out, ricochetors today are found, almost without exception, in arid regions, and it is in such regions that they have developed their highest degree of specialization. It seems likely that such a form as the modern *Zapus*, living in forested regions, but yet a ricochetor, has moved into its present environment after developing the ricochetal ability elsewhere. Moreover, Hatt (1932, p. 626) says that the jumping mice do not ricochet as much as do the Jerboas and Kangaroo Rats.

The Great Plains of the late Miocene to early Pliocene were not a desert, but they were undoubtedly becoming progressively more arid. It is thus interesting to note the beginnings of the development of ricochetal forms at such an early stage, and as soon as the country became fitted for the development of such a type. It is likely that the acquisition of ricochetal ability, once it was sufficiently pronounced to be of definite use, would proceed with considerable rapidity, as opening up an entirely new field of possible evolution, and a new facies into which to move. It seems clear that evolution is likely to proceed with an extreme of rapidity under such conditions. The Valentine and Devils Gulch facies in which *Cupidinimus nebraskensis* and *Diprionomys agrarius* were found are very sandy, and bear much more resemblance to the sandy soil so much favored by *Dipodomys* and *Microdipodops* than to the clay facies of the earlier Tertiary of the Great Plains. Of course, sandy deposits were formed earlier in the Tertiary, but they were much less widespread, and the conditions of aridity necessary for the attainment of ricochetting had not been established. It is remarkable how short a time intervenes between the appearance of climatic and environmental conditions suitable for the development of ricochetors, and their actual appearance as fossils. This is another addition to the large number of known instances where the rate of evolution in a given phylum varies markedly from one period to another. For this reason, dating of past events in years on the basis of the amount of evolution in a given group of animals, assuming a uniform rate for that evolution, must necessarily be an entirely inaccurate method of procedure, giving a fallacious appearance of scientific accuracy to results based on questionable initial assumptions.

All members of the Dipodomyinae and Perognathinae are, and were, so far as known, inhabitants of arid to desert regions. The Heteromyinae are more fond of moist, warm climates, although one species of *Proheteromys*, two of *Peridiomys*, and two of *Diprionomys* are known from the Miocene and Pliocene of western United States, which was relatively arid. Whether the species of *Proheteromys* and *Peridiomys* were better adapted to subarid conditions than were their brethren, or whether they occupied moister niches surrounded by more arid regions, we do not know. The fact that they left no known descendants suggests the latter explanation, whereas the richochetal character of the closely related *Diprionomys* indicates an attempt to become adapted to the new environment.

The distribution of the Heteromyidae (Maps, figs. 154-157) suggests certain comments on Matthew's views on distribution (Matthew, 1915). The forms occupying the southern sections of the present range of the family, and those which invaded Florida in the Miocene, all belong to the subfamily with the most primitive skeletons, the subfamily which became least adapted to the arid climate of western North America, but, on the other hand, to the subfamily with the most complicated tooth pattern. Furthermore, it may be pointed out that *Heteromys*, which is definitely less primitive than *Liomys*, occurs further to the south and further from the center of distribution of the family. *Perognathus*, which is more primitive than either *Dipodomys* or *Microdipodops*, extends further north than either. It is true that, on the whole, the more advanced members of the family have the more northern habitat. The Geomyidae, which, as a family, are more specialized than the Heteromyidae, have a lesser southern extent than do the latter, though most of the ranges of the two families overlap. Matthew (op. cit, p. 229) considers the fact that the Geomyidae do not reach South America an instance in support of his theory of northern centers of distribution for mammals, with crowding of the more primitive forms to the south. There is no doubt that, in a large number of cases, such does occur, and that, on the whole, the more northern groups are the more advanced, but it is by no means an invariable rule; it is merely a useful description of the observed results in those cases where these results *are* observed. The distribution of the genera of geomyids (Merriam, 1895) seems an exception to Matthew's rules, the Central American genera being the most specialized, while those found in the United States are more primitive, and the only genus to reach Canada is the most primitive living member of the family. The results seem to indicate that animals occupy the ecologic niche for which they are best fitted, regardless of whether they must migrate to the north or to the south to reach it, and regardless of whether they are more or less specialized than the related (or unrelated) types living immediately to the north or south.

It is also noteworthy that, during the Miocene, the Heteromyinae had the widest distribution of any of the subfamilies. Whether some

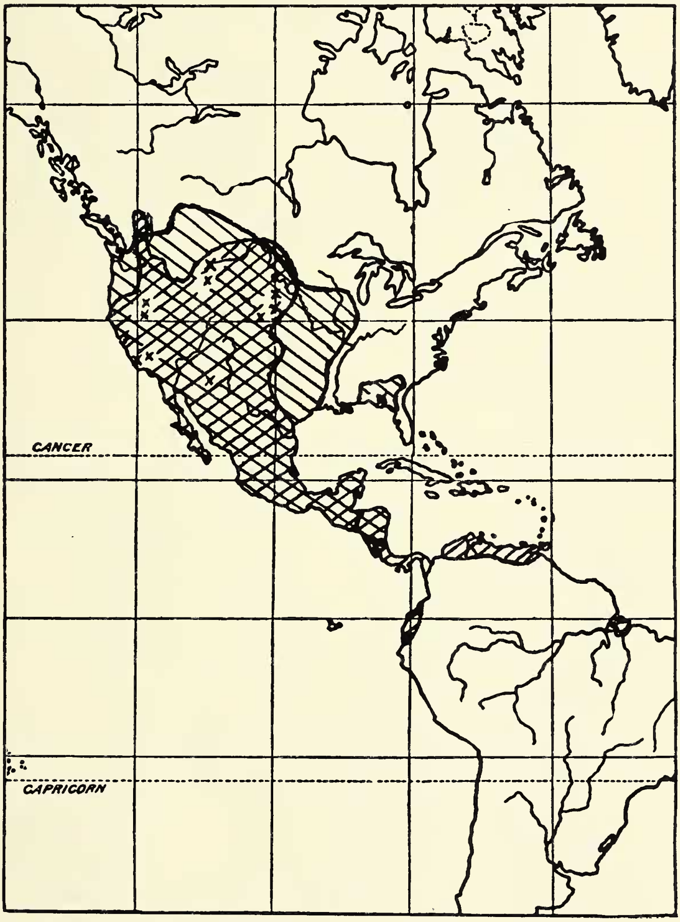

Fig. 154. Distribution of Geomyoidea. (Geomyidae after Merriam, 1895).

▧ Geomyidae.
▨ Heteromyidae.
× Fossil occurrences of Heteromyids.

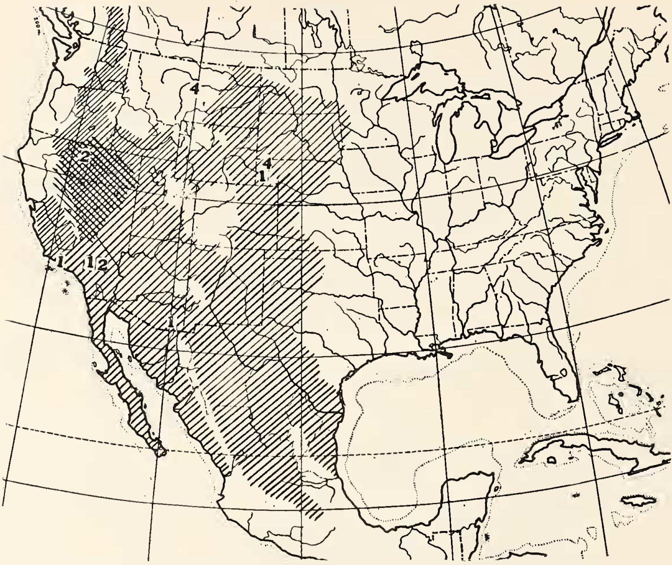

FIG. 155. Map showing distribution of Perognathinae.
///// = *Perognathus.* \\\\\ = *Microdipodops.*
1 = fossil *Perognathus.* 2 = *Perognathoides.* 4 = *Mookomys.*

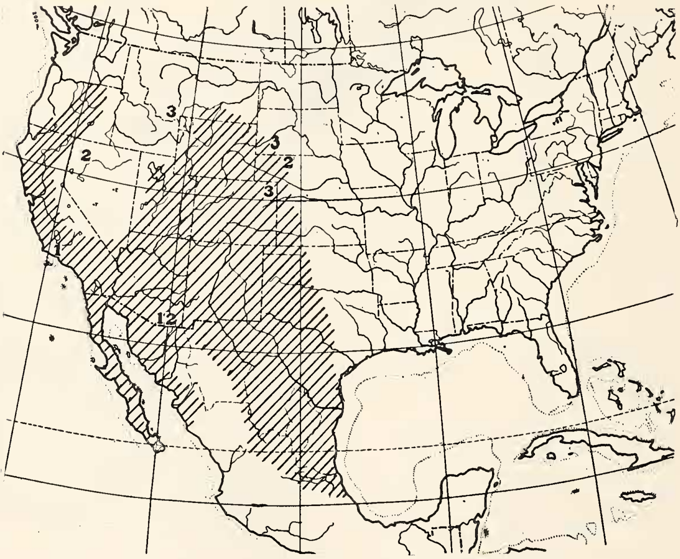

FIG. 156. Map showing distribution of Dipodomyinae.
//// = *Dipodomys.*
1 = fossil *Dipodomys.* 2 = *Cupidinimus.* 3 = *Heliscomys.*

FIG. 157. Map showing distribution of Heteromyinae.

//// = *Liomys.*

═══ = *Heteromys.*

1. *Proheteromys floridanus.*
2. *Proheteromys magnus.*
3. *Proheteromys parvus.*
4. *Peridiomys rusticus.*
5. *Peridiomys oregonensis.*
6. *Diprionomys agrarius.*
7. *Diprionomys parvus.*

members of this group were forced into Florida, and related forms were forced into Mexico and Central America by more severe competition with better adapted forms in the northern regions, or by incipient refrigeration, or whether the Heteromyines were the best fitted for the struggle for existence in the Miocene, and so spread over the whole range of the family and invaded outlying districts, can only be determined at present by an appeal to the individual's philosophy of migration and evolution. But, as pointed out by Wood (1932, p. 49), it is certainly suggestive that the fossils found in the most nearly tropical region, and in the most forested and moistest environment, are more nearly related to *Heteromys* and *Liomys* than to any other living genera.

The near coincidence of the geographic distribution of the Heteromyidae with that of the Geomyidae was first, I believe, pointed out by Murray (1866), who considered this an important reason for believing the two families to be closely related.

When they were first discovered, the different heteromyids were distributed among the groups of "Myomorphs" to which they showed the greatest superficial resemblances. *Heteromys* was first described as an aberrant species of *Mus*, serving to unite that genus with *Echimys* (Thompson, 1815). *Perognathus* was considered also to be related to *Mus*. *Dipodomys*, Gray (1841) described as the American representative of the Jerboas. Similar relationships were postulated for its synonym, *Macrocolus* (Schreber, 1846; Wagner, 1846 and 1848). The Geomyidae were, at the same time, considered related to *Arvicola* (Waterhouse, 1839), to *Bathyergus* and *Spalax* (Waterhouse, 1841), to the Spalacidae (Gray, 1843), a doubtful group of uncertain position (Waterhouse, 1848), highly specialized squirrels (Gervais, 1849), or a group between the Sciurini and Murini (Brandt, 1855). The first person to link *Geomys* and its relatives with the heteromyids was Waterhouse (1848), whose group Saccomyina was essentially equivalent to the modern term Geomyoidea. This grouping was not followed by most other authors for twenty years, although Baird (1857), Lilljeborg (1866) and Carus (1868) use essentially the same system. LeConte (1853) considered the heteromyids close to *Myoxus*, and pointed out that *Dipodomys* was no relation to the Jerboas, although Waterhouse, by implication, had anticipated him in the latter idea. The first use of a family term for the heteromyids and geomyids was by Baird (1857), who coined the term Saccomyidae. Carus (1868) subdivided this family into Saccomyina and Geomyina, synonymous with the modern families. Gray (1868) used the term Heteromyina, pointing out that *Saccomys* Fr. Cuvier 1823 is a synonym of *Heteromys* Desmarest 1817.

Gill (1872) was the first to recognize two distinct though closely related families, the Saccomyidae and Geomyidae, included under his superfamily Saccomyoidea, between Sciuroidea and Myoidea. Following Gray, Alston (1876) changed the family name from Saccomyidae to Geomyidae, with two subfamilies, Geomyinae and Heteromyinae. Coues (1875*a*; 1875*b*; 1877, pp. 488-489) disagreed as to the necessity of changing the name Saccomyidae, although admitting *Saccomys* to be a synonym, and used Baird's terminology, but following Gill in raising the subfamilies to families. Winge (1887 and 1924) apparently agreed with Coues, still using the term Saccomyidae, in which the Geomyini are a subfamily. A more complete discussion of the history of classification of the Heteromyidae is given by Coues (1877, pp. 487-491). He considers these rodents to be Myomorphs. Allen and Chapman, the first to use the term Heteromyidae (1899, p. 233), placed these rodents, in their list of the fauna of Trinidad, between the Muridae and the Octodontidae. During the present century, the general tendency has been to include the Geomyoidea among the Sciuromorpha. Even Miller and Gidley (1918), who disagree with other classifications in so many respects, include the Geomyidae and Heteromyidae in their superfamily Sciuroidae. Present conservative opinion as to the systematic position of these families is represented by Simpson (1931). Frechkop (1933, p. 12) states that the tooth pattern of the Heteromyidae is a closer approach to that of Myomorphs than to that of the Sciuromorphs. The evolutionary development of heteromyid cheek teeth seems to me, however, to be rather distinct from that of any other rodents except the Geomyidae. The type of zygomasseteric region is definitely Sciuromorphine. The presence of a premolar is also a Sciuromorph character, practically all Myomorphs having lost this tooth. Hence, for the present, the Sciuromorpha may be retained as a group containing the Sciuroidea, Geomyoidea, and possibly the Castoroidea. The relationships of the various extinct families sometimes referred to this suborder, and of the Aplodontiidae, are still uncertain.

The most striking feature of agreement between the Heteromyidae and the Geomyidae is the presence in each of cheek pouches, external to the mouth and lined with fur, which run back to the shoulder region. These are formed by an invagination of the skin of the cheeks, and are supplied with muscles derived from the platysma and other facial muscles. Murray (1866, p. 271) believed the pouches to be homologous to the internal pouches of cricetines, differing in that the hair of the face had moved into the mouth, and now lined the pouches. There is, of course, no evidence to support this idea. These pouches are capable of great distension, sometimes being swollen until they are larger than the rest of the head. The emptying of the pouches requires the use of the hands, according to most authorities, although Webster (1897) states the contrary. The earliest authors thought that the cheek pouches were capable of being turned entirely inside out, thus emptying their contents, and that the animal could walk along with these hanging down beside his head in a ludicrous manner (see Lucas, 1928, for a reproduction of an early figure). The cheek pouches can only be everted in this manner after the animal has been skinned and the pouch muscles cut.

In both families, the infraorbital foramen has migrated forward, impelled by the growth of the masseter, but it is not separated from the muscle by any crest or ridge. In both groups it now lies on the rostrum, about half way between the zygoma and the incisor. In both, the mastoid is inflated. The dental formula, $I\frac{1}{1}$, $C\frac{0}{0}$, $P\frac{1}{1}$, $M\frac{3}{3}$, is the same in both families. In both, the teeth were originally bilophed, usually with a series of three cusps in each loph. The more specialized members of each family tended toward hypsodonty and the decrease of the proportionate importance of the cusps and increase in the importance of the lophs. In both groups, the median valley then disappears, leaving a tooth composed only of an enamel oval, after but little wear. There is a tendency for antero-posterior compression of the teeth, resulting in the anterior and posterior enamel faces becoming sub-parallel, which is followed by the reduction and loss of the enamel at the two ends of the tooth, leaving two separate enamel plates. In both, P_4 tends in more specialized types to develop a multiplicity of lophs. Grooved incisors have been independently derived several times in each family. Numerous other resemblances are listed by Coues (1875*a*; 1875*b*; 1877, p. 493).

There seems to be little doubt as to the fundamental relationships of the two families. All modern authorities agree in uniting them. Their common ancestor has not, however, as yet been identified, unless further study should prove *Heliscomys* to be ancestral to the geomyids as well as to the heteromyids, which seems improbable in view of the great morphological gap between the Middle Oligocene *Heliscomys* and the John Day geomyids. Several authors, including the present writer, have suggested relationships between various fossils and the Geomyoidea, which it would be well to look into, briefly.

Wood (1933) tentatively suggested that the origin of the heteromyids might be sought in a form such as *Sciuravus nitidus* of the Middle Eocene. Further study has shown that there is very little likelihood that this form could be the ancestor of *Heliscomys*, as the cusps are tending toward a pattern of the *Ischyromys* type, with crests running toward the center of the tooth, instead of developing conical cusps as must have been the case in the ancestors of *Heliscomys*.

Moreover, although the upper molars are becoming bilophodont, the lophs consist of the primary cusps and the conules, instead of the primary cusps and styles, as in *Heliscomys*. There is no trace whatever of a cingulum in the upper teeth of *S. nitidus*. Nor is there any trace of the conules in *Heliscomys*. The crests running from the cusps of the lower teeth to the center of the basin tend to unite to form a central cusp, as in *Adjidaumo* and *Cricetids*, which is entirely absent in *Heliscomys*. Nor is any trace of a cingulum present on the lower teeth of any *Sciuravus* that I have seen.

When *Sciuravus nitidus* is thus eliminated as a possible Eocene ancestor of the heteromyids, there remains no possibility of drawing the phylogenetic line into the Eocene with any certainty whatever. It is extremely probable that some form of "*Paramys*" or a closely related genus would be the Lower Eocene ancestor of the heteromyids as well as of all other rodents, but the connecting links between this and the Middle Oligocene stages remain to be discovered.

Protoptychus, from the Uinta Eocene, has sometimes been considered a heteromyid, although Scott (1895) showed its distinctness from both heteromyids and geomyids. The tooth pattern is, indeed, suggestive in its general outline of that of the later Geomyoidea, but the details do not seem to bear out this general suggestion. The teeth of *Protoptychus* are more hypsodont than are those of any known heteromyid until the Upper Pliocene forms of *Dipodomys* are attained, and so are much more advanced than are those of *Heliscomys*. The accessory enamel lakes on the crown as shown in Scott's figure (1895, fig. 3) strongly suggest a four-lophed tooth, the anterior and posterior lophs being derived from cingula. This suggests something on the order of *Ischyromys* or *Adjidaumo*, or several other Eocene and Oligocene forms. This pattern is slightly more suggestive of "Sciuromorph" than of "Myomorph" affinities, but occurs in all suborders. As Eocene "Myomorphs" and "Sciuromorphs" are difficult to separate, this pattern would not disbar *Protoptychus* from ancestry to the Dipodidae on these grounds, although, without having particularly studied this aspect of the problem, it seems entirely possible, to me, that *Protoptychus* may represent an aberrant and sterile offshoot of the *Ischyromyidae*.[6b] The same dental divergences which prevent *Prot-*

[6b] Since writing the above, I have seen Schaub's fine monograph on the Dipodids (1934) which establishes a phylogeny for that family which rules it out from relationship with *Protoptychus*. Schaub's work on the Jumping Mice (1930) has likewise eliminated them from affinities with *Protoptychus*.

optychus from being ancestral to the Heteromyidae also separate it from the Geomyidae. The details of the skull are quite different from those of these last two families.

Numerous authors have considered *Adjidaumo* (=*Gymnoptychus*) to be related to the heteromyids, though on what grounds I am not certain. Winge (1887 and 1924) made it a member of a separate subfamily, Gymnoptychini, together with the Saccomyini and Dipodomyini forming the Saccomyidae. Scott (1895, p. 286) included the genus among the heteromyids, though without stating his reasons. Matthew (1903, p. 215), describing new material from Pipestone Springs, Montana, stated that *Gymnoptychus* and *Heliscomys* are much alike and "combine characters of Sciuridae, Geomyidae, and Heteromyidae with others peculiar to themselves or shared by the Ischyromyidae. The dental pattern strongly suggests that of *Ischyromys*, but the resemblance may be superficial; by simplification and hypsodonty it might be converted into a Heteromyid pattern. I place the genus in this family [Heteromyidae] on Scott's authority." The figure of "*Gymnoptychus*" *minimus* which Matthew gives (1903, fig. 11) shows considerable resemblance to *Heliscomys*, and would warrant the belief that this species, at least, is a close relative of the heteromyids, were it not for the fact that the figure is inaccurate, the actual pattern of the teeth of the specimen being much more like that of *Adjidaumo minor* (Matthew, 1903, fig. 10). Unfortunately, it is this incorrect figure which has been reproduced by Osborn (1907, fig. 106). Matthew (1910) considers *Gymnoptychus* to have been the common ancestor of both Heteromyidae and Geomyidae. Miller and Gidley (1918) make it the type and only genus of a new family, the Adjidaumidae. Wood (1931, phylogenetic chart), following Matthew, considered *Gymnoptychus* as the stem form of the Geomyidae, definitely ruling it out of the Heteromyidae. It is now apparent, however, that there is no available evidence justifying the assumption of any relationship between *Adjidaumo* and the Geomyoidea. As Matthew said (1903, p. 215), "The dental pattern strongly suggests that of *Ischyromys*, but the resemblance may be superficial." Further than that, I am not prepared to go at the present time. For accurate figures of the teeth of Adjidaumidae, see Burke, 1934.

Paleontologists in general have long assumed that *Paramys* represents essentially the stem form of the rodents (see especially Matthew 1910). Miller and Gidley, in their classification of the order, based on the characters of the infraorbital foramen, masseter muscle, and associated bones, believed that they discovered five types of zygomasseteric structure, none of which ever lead to any other (1918).[7] On the basis of this lack of intermediate stages between the groups, they separated forms that had long been considered to be in the relation of ancestor and descendant, placing them in different superfamilies. Matthew (see particularly Matthew and Granger, 1923, p. 4 and Matthew, 1924, footnote, p. 81) disagreed with their conclusions, and continued to follow the previously existing school of classification, but did not attempt a detailed discussion of the ideas advanced by Miller and Gidley. Matthew and Granger (1923) figure a skull of *Cricetops* whose dentition apparently indicates relationship to the Cricetidae, but whose infraorbital foramen would necessitate its inclusion among the Dipodoidae, so that they erect the family Cricetopidae for it. Schaub (1925) also noted the difficulty in finding a satisfactory niche for *Cricetops* in Miller and Gidley's classification, and considered it merely a primitive member of the Cricetidae, whose zygomasseteric structure was nearer that of *Paramys* than was that of the later members of the family.

In the earlier part of this study, I have used *Paramys* freely in comparison with the heteromyids, intending it as an example of a primitive rodent. In this respect, it is certainly useful. If, however, it could be shown that there is a strong presumption in favor of its standing in, or close to, the position of ancestor to the heteromyids, the significance of the comparisons would be greatly increased. *Paramys* is included by Miller and Gidley in the Dipodoidae, while the Heteromyidae are placed in the Sciuroidae. The critical point in their classification seems to be whether or not transitional forms occur between one type of zygomasseteric structure and another, especially within an admittedly closely related group. As the features on which their classification is based are either the anatomy and position of the masseter muscle, or features governed by its anatomy and position,

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[7] Matthew (1910, p. 68) says that "in view of the importance which the characters of this region [antorbital region] assume in the classification of rodents, and of the antiquity of this distinction [between forms with the masseter on the face and those with it confined to the zygoma] among the Sciuromorphs, I think it should be the primary basis of division in this group of the order." This statement is worth considering in connection with Miller and Gidley's classification, showing what great divergence can be reached starting at or near a common point.

it is obvious that the classification is valid only if no member of one group has developed variations in the anatomy or position of the muscle identical with, parallel to, or analogous with, the primary variations of other groups. That the Rodentia as a whole are honeycombed with parallelism has long been admitted. The Heteromyidae serve as a beautiful warning to anyone attempting a classification of the order. They clearly show that no one character can be used to the exclusion of all others, but that, to be natural, a classification must cover all aspects of the problem. They serve as a further example, if any additional ones were needed, that similar structures may be acquired independently many times, and that the end stages may only be separable by careful and detailed study of a large series of intermediate forms.

There are several instances within the heteromyids of one or more muscles changing their positions with accompanying modification of the adjacent bones. The close resemblance of the areas of muscle attachment on the humerus of *Diprionomys* to the corresponding areas in *Dipodomys*, while being quite distinct from those in *Heteromys*, can only mean that, in either *Diprionomys* or *Heteromys*, there has been a change of position and size of such muscles as the deltoids, bringing about a corresponding modification of the bones. As the infraorbital foramen is further forward in *Dipodomys* than in *Perognathus*, it seems clear that it must have moved, in the former genus, still further from the zygoma than it has in the latter. If it has moved this additional distance, why could it not originally have moved from the zygoma, where it is in *Paramys*, onto the face, as in sciurids? But the most striking action of muscle on bone detected within the family is the modification of the skull of *Microdipodops* (see above, p. 112) brought about by the migration of the temporalis muscle, and forming a distinct temporal fossa in the lateral margin of the parietal, bounded in front by a noticeable post-orbital process between it and the orbit.

This should warn us to expect similar modifications when the masseter migrates. As the migration of the latter is greater, the resulting modifications of the skull should likewise be greater. Most authorities, I believe, would admit that the migration of the temporalis described above has little phylogenetic significance, and has occurred relatively recently, starting from the condition found in the other members of the family. Why should similar, though admittedly greater, migrations of the masseter be regarded as the only sure basis for classification of the rodents, outweighing all other points of resemblance and difference, even admitting the migration of the masseter to have occurred much earlier in the evolution of the order than the movement of the temporalis described in the case of *Microdipodops?* Why could the same type of migration of the masseter not have occurred independently two or more times, if the same type of cheek tooth modification (the "*Ischyromys* pattern") has been developed independently a half dozen to a dozen times? The modification of the skull in *Microdipodops* produced by the migration of the temporalis makes the skull very similar in this region to that of the smaller genera of sciurids—an independently acquired pattern.

A rodent with the primitive type of zygomasseteric structure could be just as closely related to one in which the masseter had begun to migrate onto the face, as in Sciuromorphs, or into the orbit and toward the infraorbital foramen, eventually to pierce the zygomatic plate, as in "Myomorphs" and "Hystricomorphs," as are *Microdipodops* and the other members of the Heteromyidae, in which the temporalis has not begun to invade the dorsum of the skull. The difference in tooth pattern between *Paramys* and *Ischyromys* is, I believe, just as fundamental as the difference in zygomasseteric structure between these two genera and *Sciurus*.

In *Paramys* and other typical Eocene rodents, the infraorbital foramen is of fair size, and is situated in the zygomatic plate of the maxillary, communicating directly with the orbit, as in "Hystricomorphs" and some "Myomorphs" and "Sciuromorphs." There is not, however, any upgrowth of the masseter, either anterior to the zygoma, on the face, or within the orbit, passing through the foramen.

In the Sciuridae, the fossa for the anterior slip of the masseter, in front of the zygoma, is very clearly demarcated—posteriorly by the zygoma and anteriorly by a well marked process, separating it from the infraorbital foramen. This last, however, is only a short distance forward from the zygoma. The Castoridae are a logical derivation from this type, with a crest instead of a knob, separating the whole of the masseteric region from the foramen and anterior facial region. There does not seem to be any satisfactory interpretation of these conditions other than on the basis of the assumption that the masseter has moved up onto the anterior face of the zygoma, lateral or posterolateral to the infraorbital foramen, and then increased in size, pressing against the nerve and blood-vessels passing through the foramen, and thus causing the development of a protective bony canal extending forward to the anterior end of the masseter.

In the Heteromyidae and Geomyidae, the masseter has moved onto the face and anterior side of the zygoma in the same manner. Its subsequent expansion has forced the infraorbital foramen forward, until at present (and the same is equally true of the earliest known skulls of any member of either family), the foramen lies well forward on the muzzle, about half way between the incisor and the premolar. There is never any strong crest or process between the foramen and the muscle, the separation being brought about by distance rather than by a protective ridge between them. There is, however, considerable individual variation as to whether or not a minute crest or process may not be present. In the Sciuridae, a complete sequence can be found in different genera and species from forms with the zygomasseteric structure almost identical with that in the Geomyoidea to ones in which a crest is developed between the masseter and the infraorbital foramen, almost comparable to that in the Castoridae. There is a strong correlation between structure and size—the larger the sciurid, the more nearly the zygomasseteric structure approaches that of the Castoridae.

Most authorities agree, at the present day, and have agreed for many years, that all these families—the Sciuridae, Castoridae, Geomyidae and Heteromyidae—belong in the same major taxonomic group—the Sciuromorpha or other equivalent term. This implies that these families with somewhat diverse zygomasseteric structure were derived either from one of themselves or from some common ancestor. There is no evidence of any sort to indicate the first alternative to be true. The common ancestor would of course have had the potentiality to evolve into any of its descendants, which means practically nothing, although implying that it was almost certainly more primitive than any of the descendants. In so far as it was more primitive, it must have had a smaller anterior section of the masseter, no knobs or crests, and a more posterior location for the infraorbital foramen, all of which represent approaches toward the type of zygomasseteric region found in *Paramys.*

In the Paramyidae and Ischyromyidae, the infraorbital foramen, though large, did not transmit any muscle. Nor was the anterior surface of the zygoma modified for the muscle. Incidentally, the infraorbital foramen is no larger proportionately than in the Heteromyidae, in which group it has not been reduced in size by compression from the masseteric region, but has been forced bodily forward ahead of the muscle. The small size and lack of specialization of the masseter are what one would naturally expect in an ancestral form. There can be little doubt that the Heteromyid, Geomyid, Sciurid, and Castorid conditions, whatever relation they may bear to each other or to those of other rodents, and whatever one may believe about the probability of deriving them from the structures represented in any particular form, are not the most primitive types of zygomasseteric structure ever occurring in the history of these families and their ancestors. Most authors would agree that the rodents are derived from the great insectivore (sensu latissimo) stock. In these, the infraorbital foramen does not transmit muscles; the masseter does not extend up onto the face in front of the zygoma; no crests are developed for it on the face; and the infraorbital foramen has not migrated forward. In other words, the arrangement is essentially that of *Paramys*. If all the diverse types of zygomasseteric arrangement have been derived from this central one at one time or another, what reason is there to assume that each one has only been acquired once, and that before the beginning of the Eocene? The more specialized types of zygomasseteric structure are not known among rodents before the Oligocene. Before this time, the separation of "Sciuromorphs" from "Myomorphs" is difficult if not impossible, suggesting very strongly that these groups are drawing toward their common ancestor. It is necessary to keep in mind the fact that the time interval from the first appearance of *Paramys* at the bottom of the Eocene to the Middle Oligocene occurrences of *Heliscomys* is equal to that from the Middle Oligocene to the present.

In studying the variation in the zygomasseteric structure of Sciuromorphs, a skull of *Tamias* was observed in which the infraorbital foramen had migrated an unusually short distance from the zygoma. This led to a further investigation, and the discovery of a most interesting series among specimens of *Tamias*, especially *T. striatus fischeri*. Thirty-two skulls of this subspecies were studied, in which all variations occurred from forms in which the infraorbital foramen had been forced somewhat forward, and a slight process developed ventrally to it, to ones in which the foramen still remained in the primitive position of the zygoma, being surrounded by the area of origin of the masseter. This type of zygomasseteric structure differs from that of *Paramys* only in that in the latter genus the masseter has not started its upgrowth. It is even closer to the condition in a skull of *Mylagaulus* sp. in the author's possession (A. E. W. No. 9145) in which, although the masseter did not extend onto the anterior face of the zygoma, the size, shape and appearance of the IOF is the same. The general structure of *Tamias* is as close to that of *Mylagaulus* as it is to that of Sciurus.

This is highly significant, as Miller and Gidley include the Mylagaulidae, with the Paramyidae, in the Superfamily Dipodoidae. It seems reasonable to assume that if the zygomasseteric structure found in the Mylagaulidae is alone sufficient to assign that family to the Dipodoidae, then the occurrence of this similar zygomasseteric structure in some specimens of *Tamias striatus fischeri* should warrant their inclusion in that superfamily as readily as in the Sciuroidae. But the structure in other specimens of the subspecies, being typically sciuroid, would necessitate their allocation to the Sciuroidae, and the drawing of a superfamilial line between different members of a single subspecies. And as all stages of the transition occur in this form, it would be an extremely difficult task to determine which specimens belonged to which superfamily. When a species is found some members of which belong to one superfamily and some to another, it is an interesting case of the way all intermediate stages are present in evolution, and shows how little nature cares for human boundaries, *if* the species is actually ancestral to both superfamilies. An approach to this condition is found among the lower Eocene Perissodactyls. But when the species in question is a late member of one superfamily, by no possibility ancestral to either group, there seems to be an error of some sort in the basis of the classification.

But aside from such transitional forms, the Superfamily Dipodoidae includes forms that are only verbally similar. The character of the zygomasseteric structure as given by Miller and Gidley ("nearly horizontal, always narrow and completely beneath infraorbital foramen" 1918, p. 439) includes widely different types, which appear to have reached their present condition in widely different manners. In *Paramys* and the Mylagaulidae, for example, the zygomatic plate is nearly horizontal because that is the primitive condition for rodents and the growing masseter has not as yet effected any great change. In the Dipodidae, on the other hand, the zygomatic plate is horizontal because the masseter has passed through the infraorbital fenestra and, on expanding, has forced the zygoma down until it becomes even lower than in the primitive forms. There seems to be no real justification for considering these two types of zygomasseteric structure to be identical.

Let us now try to visualize the ancestral forms for the different types of zygomasseteric structure found in some of the various recent rodents. The ancestor of the Sciuromorpha must have been a form in which the masseter had not started to enlarge on the face, and was confined to the zygoma. The zygoma was probably nearly horizontal its position not yet having been altered by the muscle. The infraorbital foramen was on the zygomatic plate, which was fairly narrow and was above the zygoma. This type is exactly represented by the Lower Eocene *Paramys*. In the "Myomorpha" and "Hystricomorpha," the ancestral form did not have the masseter passing through the IOF, but it was confined to the zygoma; the IOF was not enlarged; the zygoma was horizontal but not as low as in the Dipodidae. This type is exactly represented by the Lower Eocene *Paramys*. In dental structure, *Paramys* could be ancestral to any of the later rodents, as was admitted by Miller and Gidley. Of course it might be possible that *Paramys* is not ancestral to all the later rodents, and that we would have to go back into the Paleocene to find the common stock. But the principle is the same in either case, as *Paramys* seems either the common ancestor, or else a very slightly modified descendant of the common ancestor, in which case it can legitimately be considered structurally ancestral. But, whatever its relationships may be to the "Myomorpha" and "Hystricomorpha," it is difficult to believe that the *Paramys* stock is not ancestral to all the Sciuromorphs.

One reason for the difficulty in reaching a firm ground for the subordinal classification of the Rodentia is the uncertainty as to what the evolution has been, in nearly every group. While many fossil rodents have been described, most of them have been in faunal papers by authors who were specialists on some other group of mammals. Furthermore, the number of fossil rodents described in proportion to the number of living members of the order is relatively small, about 8% of the fossil mammals listed in Hay's two catalogues of North American Fossil Vertebrates (1902 and 1930) being rodents, whereas about 55% of the recent mammals listed by Miller are rodents (1924). Other than the Cricetidae and Dipodidae, no detailed phylogenetic studies of any group as a whole, with sufficient material to make the results reasonably valid, have been published. In the two families listed above, the evolutionary work has been limited to parts of the family, and large quantities of other material has been essentially untouched. Schaub's fine monograph has placed the European Cricetinae, at least, in a fairly understandable position. It is hoped that this study will help to put the Heteromyidae in a similar position.

A further difficulty in the way of correct interpretation of the evolutionary trends and stages is the lack of described skull and skeletal material, most fossil rodents being known from teeth and jaws alone.

And finally, while the modern families of rodents may be traced back to the Oligocene with greater or lesser success, and Eocene groups have been discovered, and sometimes traced into the Oligocene, the connecting links between the two groups have rarely, if ever, been identified and clarified.

There is much evidence that a fourfold division, or even greater multiplicity of superfamilial groupings, is necessary for a correct visualization of the relationships of the order. One of the most useful features of Miller and Gidley's classification (and there are many) is the emphasis on the polyphyletic nature of the rodents. But it is difficult to believe that the arrangement of many of the families as indicated by Gill, Tullberg and others in the latter part of the last century was not a closer approximation to the truth than that adopted by Miller and Gidley.

In conclusion, I wish to quote from Matthew and Granger (1923, p. 4), as follows: "No interpretation of the affinities of existing and extinct rodents can avoid the assumption of a large amount of parallelism, but it would seem that Messrs. Miller and Gidley have carried it to improbable extremes in support of certain preconceived theories of what can or cannot occur in the modification of the zygomatic and dental construction, and that a reasonable application of the law of probabilities to what we know of fossil rodents would lead to some modification of these theories and a resultant simplification of their otherwise admirable revision, which we fully recognize as based upon a most thorough and complete review of the whole order, particularly as including the extinct as well as the existing genera."

To summarize, it seems established that:

(1) the zygomasseteric structure of the Paramyidae is primitive;

(2) that of such modern rodents as the Sciuridae, Castoridae, Geomyidae, Heteromyidae, etc., is not;

(3) these latter types must have been derived from a form with the general zygomasseteric structure found in *Paramys*;

(4) *Paramys* in its other characters could be a common ancestor to the later forms;

(5) its time relations are correct for an ancestor;

(6) no other known form could possibly represent the common ancestor, since the only other competitor, in point of time, *Eurymylus*, is apparently not a rodent at all.

It is impossible to over-emphasize the tremendous amount of parallelism which has flooded the evolution of the rodents. There is far and away a greater amount in this order than in any other order of mammals, and perhaps nearly as much as in all other placentals. The reason for this is not hard to find. The rodents are an order equal to all other mammals in numbers of individuals and of species. The common ancestor of all these forms is much more recent than the common ancestor of other mammals. The habitats, food, size, and locomotor habits of the group are much more uniform than is the case with the rest of the mammals. If, as seems certain, the closer the relationship; the closer the food habits; the closer the locomotor habits; the closer, in fact, the whole environment of two groups is, the greater the number of parallel mutations, and hence the greater the parallelism in evolution, it is not surprising that the rodents show such a wonderful example of what may be termed "parallel radiation."

CONCLUSIONS

1. The Heteromyidae developed numerous branches during the middle and later Tertiary, which have paralleled each other to a high degree. These lines fall into three main groups, to which are applied Coues' subfamily names. The Heteromyinae are more distinct than are the other two groups.

2. The ricochetal ability has been acquired at least two, probably three, and perhaps more, times within this family. The high inflation of the skull has occurred an equal number of times. Fusion of cervical vertebrae is only known to have been developed in two genera.

3. The cheek tooth patterns are quite distinct in the various genera, and frequently can be used to distinguish the different species of living

heteromyids, especially when unworn teeth are available. This is clearly shown in the case of *Dipodomys*, of which a more detailed study was made than of the other living genera. The teeth of this genus are closely parallel to those of the Geomyidae in the restriction of the enamel to the anterior and posterior faces of the tooth.

4. All members of the family are considered descended from *Heliscomys* of the Middle Oligocene. No other known forms from Oligocene or earlier horizons can be assigned to this family or considered closely related to it.

5. The common ancestor of the geomyids and heteromyids has not yet been found.

6. Frechkop's hypothesis of "homodynamie renversée" is shown not to be an elucidation of homologies, but, merely, a description of superficial resemblances.

7. *Paramys* seems to be the ideal ancestor for the heteromyids as well as for other rodents. The hypotheses of Friant and Schreuder for derivation of rodents from Multituberculates by way of Hystricomorphs appear entirely erroneous, due to incorrect initial postulates.

8. Miller and Gidley's classification of rodents on the basis of the structure of the zygomasseteric region is considered untenable, as it is based on a single character, neglects the modifications of the bone brought about by the enlarging of the masseter muscle, and is opposed by all the evidence of paleontology, as well as by much evidence drawn from recent rodents. In spite of this, it is unquestionably the best classification that has yet been made.

9. The most important point to be emphasized is that "Parallelism, parallelism, more parallelism and still more parallelism" is the evolutionary motto of the rodents in general and of the heteromyids in particular. This extends to all parts of the body. It makes the task of determining interrelationships particularly difficult, and renders exceptionally dangerous any postulates as to what the relationships of a given form may really be, if full evidence does not exist to clear the maze of parallel adaptations for us. This shows the insuperable difficulties awaiting anyone who attempts a classification based on a single character or on a group of characters with a common cause. The parallelism is so great that there is no justification for believing two apparently identical structures to be the same, unless the apparent identity is supported by apparent identity of many other structures, or unless the development of the two characters can be traced through

and proven to be identical at every step. As it has not been possible to trace the complete sequence of heteromyid evolution, there are undoubtedly many errors of interpretation in the present work. "Parallel radiation" is used as a descriptive term of the type of evolution represented by the rodents.

Previously, the only group of rodents sufficiently well known to warrant any belief in an understanding of such a simple item as cusp homologies in the different members was the Cricetinae, monographed by Schaub. It is hoped that the present work will bring another group of rodents toward the point where we can have a similar understanding of its evolution.

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